Instytut Dendrologii Polskiej Akademii Nauk

mgr inż. Sonia Paź-Dyderska

Cechy reprodukcyjne roślin drzewiastych jako narzędzie ekologii funkcjonalnej: analiza zmienności i potencjału

Reproductive traits of woody plants as a tool for functional ecology: analysis of variability and potential

Praca doktorska
wykonana w Zakładzie Ekologii
Instytutu Dendrologii Polskiej Akademii Nauk

Promotor: prof. dr hab. inż. Andrzej M. Jagodziński

Kórnik, 2024

Badania zostały sfinansowane ze środków Narodowego Centrum Nauki w ramach grantu Preludium nr 2020/37/N/NZ8/00387 pt. „Jak lepiej opisać funkcjonowanie gatunków w ekosystemie? Cechy reprodukcyjne i ich potencjał w ekologii funkcjonalnej roślin”, a także w ramach zadania badawczego nr 2021/01/ZB/FBW/00003 pt. „Słodko-gorzkie życie kwiatów. Zmienność zawartości cukrów i fenoli w kwiatach drzew i krzewów strefy klimatu umiarkowanego”, sfinansowanego przez Instytut Dendrologii PAN w ramach Funduszu Badań Własnych oraz w ramach badań statutowych Instytutu Dendrologii PAN.

Rodzicom

Podziękowania

Rodzinie, przyjaciołom i wszystkim osobom, które wspierały mnie w naukowym rozwoju, serdecznie dziękuję. Cieszę się, że towarzyszyliście mi w tej wędrówce.

Pragnę złożyć gorące podziękowania **Profesorowi Andrzejowi M. Jagodzińskiemu**, z którego fachowej wiedzy czerpię już od czasu przygotowywania pracy inżynierskiej. Dziękuję Panu za wyrozumiałość, a także za swobodę badawczą, która pozwoliła mi odkrywać i zgłębiać różnorodne zagadnienia z zakresu ekologii roślin, przyczyniając się do poszerzania moich horyzontów.

Serdecznie dziękuję wszystkim koleżankom i kolegom z **„Budynku D"**. Szczególnie dziękuję **Katarzynie Rawlik** za chętne dzielenie się nie tylko wiedzą, ale też entuzjazmem, a także za nieustanne wsparcie na nierzadko wyboistej drodze kariery naukowej. **Romie Żytkowiak** bardzo dziękuję za bezcenną pomoc przy organizacji całego procesu badawczego. Za rozwijające dyskusje, praktyczne wskazówki dotyczące rzetelnego prowadzenia badań naukowych, a także za cięty dowcip i pogodę ducha serdecznie dziękuję **Dawidowi Adamczykowi**, **Sebastianowi Buremu**, **Pawłowi Horodeckiemu** oraz **Francesco Latteriniemu**. Za wartościowe rozmowy dziękuję **Olenie Blinkovej** oraz **Quadriemu Anibabie**. Paniom **Agnieszce Drewniak**, **Paulinie Dudek-Zychar**, **Zofii Kozłowskiej**, **Dorocie Skwaryło**, **Elżbiecie Szubert** i **Róży Walkowiak-Bułaj** dziękuję za życzliwość oraz pomoc w pracach laboratoryjnych, a także za cenne rady dotyczące planowania prac terenowych.

Za pouczającą współpracę, a także za dzielenie się doświadczeniem badawczym, serdecznie dziękuję **Radosławowi Puchałce**, **Patrykowi Czortkowi** oraz **Łukaszowi Dylewskiemu**.

Dziękuję Pani **Kindze Nowak** za pomoc przy projektowaniu i realizacji badań składających się na niniejszą rozprawę. Pani profesjonalizm i wiedza przydały jej wartości.

Dziękuję wspaniałym nauczycielkom i nauczycielom, których spotkałam na swojej drodze. W szczególności dziękuję Pani **Arlecie Kaźmierczak**, która swoją dociekliwością i poczuciem humoru zaraziła mnie już w gimnazjum. Dzięki Pani weszłam w dorosłość z wiarą w siebie, która dodała mi skrzydeł. Dziękuję Pani **Renacie Borowiak**, która z właściwą sobie swadą pokazała mi, jak wielką moc sprawczą mają słowa i opowieści.

Dziękuję **Marcie Talarczyk** za pozytywną energię i odrobinę szaleństwa, a także za wiarę we mnie już od kilkunastu lat.

Chciałabym z głębi serca podziękować **Mamie** i **Tacie**, a także ukochanym **Dziadkom**, za bezwarunkową miłość, ciągłe wsparcie i radosne dzieciństwo. Dziękuję za czas, który mi poświęciliście, a także za rozbudzenie zainteresowania światem przyrody. Dziękuję siostrze **Martynie** za dzielenie radości i trudów okresu dojrzewania, a także za prawdziwie siostrzaną więź, którą czuję każdego dnia.

Dziękuję mojemu największemu kibicowi – mężowi **Marcinowi**, za niewyczerpane pokłady miłości i cierpliwości, dzielenie pasji, a także za radykalne wsparcie na wszystkich etapach przygotowania tej rozprawy.

Spis treści

Lista publikacji stanowiących rozprawę doktorską

Wyniki badań zostały opublikowane w następujących artykułach naukowych:

1. **Paź-Dyderska S.**, Jagodziński A.M. 2024. Low intra-canopy variability of floral traits in temperate woody plants. Global Ecology and Conservation 54, e03054. https://doi.org/10.1016/j.gecco.2024.e03054
2. **Paź-Dyderska S.**, Żytkowiak R., Jagodziński A.M. 2022. Intra- and Interspecific Variability of Non-Structural Carbohydrates and Phenolic Compounds in Flowers of 70 Temperate Trees and Shrubs. Forests 13, 1256. https://doi.org/10.3390/f13081256
3. **Paź-Dyderska S.**, Jagodziński A.M. 2024. Potential of reproductive traits in functional ecology: A quantitative comparison of variability in floral, fruit, and leaf traits. Ecology and Evolution 14, e11690. https://doi.org/10.1002/ece3.11690

Abstract

Plant functional traits are tools in functional ecology that enable the development of models concerning the current and future functioning of ecosystems. In the context of ongoing climate change, such predictions are essential. However, many studies to date have been based on the concept of the plant economics spectrum, which primarily considers leaf and shoot traits. Recently, more researchers have been advocating for the inclusion of traits representing all plant organs to better understand species and ecosystem functioning. This study aspires to fill this gap.

The aims of the study were (1) to analyze the variability of selected floral and fruit traits at both interspecific and intraspecimen levels, and (2) to determine the potential of these traits for functional ecology. We hypothesized that: (H1) reproductive traits will be strongly correlated with phylogeny, (H2) reproductive traits will show less intraspecimen variability than interspecific variability, (H3) reproductive traits will have lower intraspecimen and interspecific variability than traits related to resource availability, commonly used in ecology, and (H4) reproductive traits will be correlated with other commonly used traits representing the global spectrum of plant form and function.

The study found a statistically significant correlation between floral size traits, as well as some chemical traits, with the evolutionary history of species (H1). Additionally, there is considerable interspecific variability in the studied floral and fruit traits, indicating a wide range of reproductive strategies among the species studied. Light availability has a low impact on the intraspecimen variability of the studied floral and fruit traits (H2). The ratio of intraspecimen to interspecific variability depends more on the specificity of the analyzed trait than on whether or not it is a reproductive trait (H3). The analyzed floral and fruit traits complement the global spectrum of plant form and function and are consistent with traits representing other plant organs (H4).

The results highlight the significant potential of floral and fruit traits for further research in functional ecology. The correlations with phylogeny, as well as the high interspecific variability alongside the strong stability of traits at the intraspecimen level, suggest that extrapolation of these trait measurements to other individuals of a given species is justified for many types of ecological research. The strong consistency of floral and fruit traits with commonly used traits of other organs encourages further studies aimed at fully understanding the diversity of forms and functions of species, with a particular focus on their reproductive strategies.

Streszczenie

Cechy funkcjonalne roślin są narzędziem ekologii funkcjonalnej, które umożliwiają między innymi opracowanie modeli dotyczących obecnego i przyszłego funkcjonowania ekosystemów. W kontekście postępujących zmian klimatycznych takie predykcje są niezbędne, jednak dotychczas wiele badań opierało się na koncepcji ekonomicznego spektrum roślin, uwzględniającej głównie cechy liści i pędów. Obecnie coraz więcej badaczy postuluje włączanie cech reprezentujących wszystkie organy roślin do badań, by lepiej zrozumieć funkcjonowanie gatunków i ekosystemów. W niniejszych badaniach skoncentrowano się na wypełnieniu tej luki.

Celem badań było (1) przeanalizowanie zmienności wybranych cech kwiatów i owoców na poziomie międzygatunkowym i wewnątrzosobniczym oraz (2) określenie potencjału tych cech w rozwoju ekologii funkcjonalnej. Przyjęto następujące hipotezy badawcze: (H1) cechy reprodukcyjne będą silnie powiązane z filogenezą, (H2) cechy reprodukcyjne będą charakteryzowały się mniejszą zmiennością na poziomie wewnątrzosobniczym niż międzygatunkowym, (H3) cechy reprodukcyjne będą charakteryzowały się mniejszą zmiennością na poziomie wewnątrzosobniczym i międzygatunkowym niż często stosowane w ekologii cechy związane z dostępnością zasobów, (H4) cechy reprodukcyjne będą powiązane z innymi, powszechnie wykorzystywanymi cechami reprezentującymi globalne spektrum form i funkcji roślin.

W toku badań stwierdzono, że istnieje statystycznie istotna korelacja pomiędzy cechami kwiatów dotyczącymi ich rozmiaru, a także niektórymi cechami chemicznymi, a historią ewolucyjną gatunków (H1). Ponadto, istnieje znaczna zmienność badanych cech kwiatów i owoców na poziomie międzygatunkowym, co wskazuje na szerokie spektrum strategii reprodukcyjnych badanych gatunków. Dostępność światła ma natomiast niewielki wpływ na zmienność badanych cech kwiatów i owoców na poziomie wewnątrzosobniczym (H2). Stosunek zmienności wewnątrzosobniczej do międzygatunkowej jest zależny od specyfiki danej cechy i nie jest bezpośrednio determinowany przez rodzaj organu, który cecha reprezentuje (H3). Analizowane cechy kwiatów i owoców uzupełniają globalne spektrum form i funkcji roślin i są zgodne z wykorzystywanymi do tej pory cechami pozostałych organów (H4).

Uzyskane wyniki jednoznacznie wskazują na znaczny potencjał cech kwiatów i owoców w dalszych badaniach z zakresu ekologii funkcjonalnej. Korelacje z filogenezą, a także duża zmienność międzygatunkowa przy jednoczesnej dużej stabilności cech na

poziomie wewnątrzosobniczym, pozwalają sugerować, że ekstrapolacja pomiarów tych cech na pozostałe osobniki danego gatunku w przypadku wielu rodzajów badań ekologicznych jest uzasadniona. Duża zgodność cech kwiatów i owoców z powszechnie wykorzystywanymi cechami pozostałych organów zachęca do podjęcia dalszych badań, mających na celu pełne zrozumienie różnorodności form oraz sposobów funkcjonowania gatunków, ze szczególnym uwzględnieniem ich strategii reprodukcyjnych.

1. Wstęp

Cechy funkcjonalne roślin to ich mierzalne parametry, które w sposób ilościowy odpowiadają nie na pytanie „kim jesteś?”, ale raczej „jaka jest twoja rola?” (Streit i Bellwood 2023). W efekcie umożliwiają między innymi opracowanie modeli dotyczących obecnego i przyszłego funkcjonowania ekosystemów (Bussotti i in. 2015; Streit i Bellwood 2023). Z tego względu ekologia funkcjonalna bywa porównywana do współczesnej kryształowej kuli, a według licznych badaczy szerokie zastosowanie cech funkcjonalnych zwiastuje początek nowej ery „ekologii prognostycznej” (ang. *predictive ecology*), która pozwoli na przewidywanie przyszłych warunków ekologicznych na podstawie obecnej specyfiki zbiorowisk (Kattge i in. 2020; Mouillot i in. 2013; Streit i Bellwood 2023). W kontekście dynamicznie postępujących zmian klimatycznych takie predykcje są niezbędne, ponieważ pozwalają na zrozumienie i ilościowe przedstawienie funkcjonowania gatunków i ekosystemów na niespotykaną dotąd skalę (Aubin i in. 2016; Kühn i in. 2021).

Dotychczas wiele badań dotyczących funkcjonowania gatunków opierało się na koncepcji ekonomicznego spektrum roślin (ang. *plant economics spectrum*, PES), która określa jak rośliny równoważą swoje inwestycje w różne procesy w zależności od dostępności zasobów i występowania czynników stresowych (Reich 2014). Ta koncepcja uwzględnia głównie cechy liści i pędów. Obecnie jednak coraz więcej badaczy postuluje włączanie cech reprezentujących wszystkie organy roślin do badań, by lepiej zrozumieć funkcjonowanie gatunków i ekosystemów (Kleyer i Minden 2015; Paź-Dyderska i Jagodziński 2023). E-Vojtkó i in. (2022) wykazali, że cechy kwiatów mogą zostać skutecznie zintegrowane z PES oraz że cechy kwiatów są w dużej mierze odrębne od PES, dostarczając nowych informacji z zakresu strategii życiowych roślin. Kompromisy dotyczące produkcji kwiatów przedstawili także Roddy i in. (2021), proponując koncepcję ekonomicznego spektrum kwiatów (ang. *flower economics spectrum*, FES), która bada czynniki wpływające na cechy i funkcje kwiatów. Główne kompromisy w ramach FES obejmują koszty produkcji i utrzymania kwiatów w odniesieniu do potencjalnych zysków, czyli wyprodukowanych nasion. Koncepcja FES sugeruje podział kwiatów na cztery podstawowe grupy: (1) tanie, krótkotrwałe kwiaty (np. rośliny ruderalne), (2) kosztowne, krótkotrwałe kwiaty (np. kaktusy), (3) kosztowne, długotrwałe kwiaty (np. storczyki) oraz (4) tanie, długotrwałe kwiaty (obecnie nieznane). Autorzy zastrzegają jednak, że do weryfikacji proponowanych strategii dotyczących kompromisów pomiędzy kosztem produkcji a utrzymania kwiatów powinny zostać wykorzystane dane empiryczne, których obecnie brakuje. Lanuza i in. (2023) wprowadzili koncepcję reprodukcyjnego spektrum roślin okrytonasiennych, a ich globalna analiza 18 cech reprodukcyjnych dla 1506 gatunków wykazała, że ponad 50% całkowitej zmienności cech jest wyjaśniane m.in. przez negatywną korelację między liczbą kwiatów a ich wielkością. Cechy reprodukcyjne dostarczają więc rozmaitych nowych informacji na temat strategii życiowych roślin, jednak potencjał wynikający z włączania ich do badań z zakresu ekologii funkcjonalnej pozostaje niewykorzystany. E-Vojtkó i in. (2020) jasno wskazują, że jedną z głównych przyczyn pomijania cech reprodukcyjnych w badaniach z zakresu ekologii funkcjonalnej jest niewystarczająca ilość danych dotyczących cech kwiatów i owoców, a pierwszy krok do pełniejszego wykorzystania potencjału tych cech mogłoby stanowić opracowanie wystandaryzowanego protokołu zbioru oraz wzmożenie wysiłków z zakresu lepszego pokrycia gatunków pomiarami w otwartych bazach danych. Pozwoliłoby to dostarczyć informacji nie tylko z zakresu międzygatunkowej, ale również wewnątrzgatunkowej i wewnątrzosobniczej zmienności badanych cech.

Obecnie temat międzygatunkowej zmienności cech kwiatów i owoców pozostaje niedostatecznie rozpoznany, choć trzeba zaznaczyć, że w ostatnich latach powstaje coraz więcej prac z tego zakresu. Przykładowo, Bentos i in. (2014) wykazali, że masa nasion, liczba nasion, masa owoców i liczba owoców różniły się aż o kilka rzędów wielkości wśród zaledwie 12 gatunków drzew. Wyniki te sugerują, jak wielką wartość informacyjną mogą nieść ze sobą dane dotyczące cech reprodukcyjnych roślin. Kwestia zmienności wewnątrzgatunkowej również przykuwa uwagę wielu badaczy, choć, jak wynika z globalnej analizy Kupplera i in. (2020), przeprowadzonej na 18401 pomiarach dla 2822 gatunków, uwzględnienie wewnątrzgatunkowej zmienności cech kwiatów i liści może zarówno poprawić, jak i utrudnić nasze rozumienie tego, jak rośliny radzą sobie w zróżnicowanych warunkach środowiskowych. Nie znamy jeszcze bowiem ogólnych, globalnych trendów, które umożliwiłyby interpretację wyników związanych ze zmiennością cech reprodukcyjnych roślin.

Zmienność cech możemy rozpatrywać także na poziomie wewnątrzosobniczym. Badania z tego zakresu dotyczące cech kwiatów i owoców są bardzo nieliczne. Dysponujemy jednak analogicznymi badaniami dla specyficznej powierzchni liści, które wykazały, że dla 179 gatunków drzew i krzewów zmienność tej cechy na poziomie wewnątrzosobniczym wyniosła 43% (Paź-Dyderska i in. 2020). Taka zmienność wewnątrzosobnicza u liści pozwala sądzić, że podobne zróżnicowanie może występować również w przypadku kwiatów i owoców. To zagadnienie zostało zbadane na przykładzie hodowlanych odmian jabłoni. Przykładowo, owoce z zewnętrznej części korony charakteryzowały się wyższą świeżą masą owocu, wyższą zawartością cukrów rozpuszczalnych oraz niższą zawartością skrobi w porównaniu do owoców z wewnętrznej części korony (Feng i in. 2014). Zmienność cech kwiatów i owoców roślin pozostaje więc tematem o ogromnym potencjale dla rozwoju ekologii roślin, udowadnianym przez pojawiające się coraz częściej nowe prace z tego zakresu (E-Vojtkó i in. 2022, 2020; Lanuza i in. 2023; Roddy i in. 2021), choć nadal niewystarczająco rozpoznanym.

2. Cele i hipotezy

Celem rozprawy doktorskiej jest **(1)** przeanalizowanie zmienności wybranych cech kwiatów i owoców (cech reprodukcyjnych) na poziomie międzygatunkowym i wewnątrzosobniczym oraz **(2)** określenie potencjału tych cech w rozwoju ekologii funkcjonalnej.

W badaniach przyjęto następujące hipotezy:

H1: Cechy reprodukcyjne będą silnie powiązane z filogenezą.
Dotychczasowe badania podkreśliły korelacje między cechami funkcjonalnymi a historią ewolucyjną gatunków, m.in. dla koncentracji węgla w drewnie (Martin i in. 2018), specyficznej powierzchni liści (Paź-Dyderska i in. 2020) czy zmienności masy nasion (Zhang i in. 2020). W przypadku cech kwiatów takie badania były do tej pory rzadkie. Tymczasem, konwergencja cech kwiatów jest stosunkowo powszechna, szczególnie w przypadku gatunków zapylanych przez funkcjonalnie podobne gatunki zapylaczy (Anderson i Johnson 2009; Bernhardt 2000). Oczekiwaliśmy więc bliskiego związku tych cech z historią ewolucyjną gatunków.

H2: Cechy reprodukcyjne będą charakteryzowały się mniejszą zmiennością na poziomie wewnątrzosobniczym niż międzygatunkowym.
Założenie to opiera się na wcześniej obserwowanej wewnątrzgatunkowej stabilności cech związanych z reprodukcją. Przyjęliśmy, że czynniki takie jak ekspozycja na światło i ciepło nie doprowadzą do istotnego zróżnicowania cech kwiatów występujących w różnych częściach korony.

H3: Cechy reprodukcyjne będą charakteryzowały się mniejszą zmiennością na poziomie wewnątrzosobniczym i międzygatunkowym niż często stosowane w ekologii cechy związane z dostępnością zasobów, tzw. *performance-related traits* (np. specyficzna powierzchnia liści, maksymalna wysokość drzewa czy zawartość azotu w liściach).
Ze względu na dużą wewnątrzgatunkową stabilność cech reprodukcyjnych spodziewamy się, że w mniejszym stopniu będą one zależne od zmiennych warunków środowiskowych.

H4: Cechy reprodukcyjne będą powiązane z innymi, powszechnie wykorzystywanymi cechami reprezentującymi globalne spektrum form i funkcji roślin (np. cechami liści lub łodyg).

Wielowymiarowe analizy przeprowadzone w badaniach E-Vojtkó i in. (2022) jasno wskazują, że cechy kwiatów są w dużej mierze niezależne od ekonomicznego spektrum liści (Wright i in. 2004) oraz że wyjaśniają unikalną część zmienności formy i funkcji roślin (Díaz i in. 2016). Zakładamy, że dodanie kolejnych cech kwiatów i owoców może zwiększyć poziom zmienności form i funkcji roślin wyjaśniany w ramach PES, co umożliwi dokładniejsze opisanie funkcjonowania gatunków w ekosystemach.

3. Materiał i metody

3.1. Teren badań

Badania zostały zrealizowane w należącym do Instytutu Dendrologii PAN Arboretum w Kórniku. Arboretum jest jedną z najstarszych i największych kolekcji dendrologicznych w Europie i stanowi dziedzictwo wielu pokoleń ludzi związanych z Kórnikiem (Jagodziński i Nowak-Dyjeta 2012; Nowak-Dyjeta i in. 2013). Najdawniejsze wzmianki o Zamku Kórnickim i otaczających go terenach pochodzą już z XIV wieku, gdy Kórnik należał do rodu Górków. Kamieniem milowym w historii parku był wiek XVIII, kiedy to pod kierunkiem Teofili Szołdrskiej-Potulickiej gruntownie przebudowano Zamek i założenia parkowe, nadając im charakter ogrodu francuskiego. Usytuowanie Zamku w pobliżu jeziora, na terenie niegdysiejszych bagien, zadecydowało o korzystnych stosunkach wodnych na terenie ogrodu, a w efekcie – późniejszych sukcesach z zakresu uprawy wielu rzadkich gatunków drzew i krzewów (Białobok 1955; Kąsinowska 2019).

Za moment powstania Arboretum uznaje się rok 1826, kiedy pieczę nad Kórnikiem objął Tytus hr. Działyński. Nie tylko powiększył on park, ale także zmienił jego charakter, urządzając go w stylu angielskim. Przede wszystkim jednak znacząco wzbogacił kolekcję dendrologiczną. Najstarsze okazy w Arboretum, osiągające wiek 180-200 lat, pochodzą z okresu jego działalności (Nowak 2020). Dzieło Tytusa z pasją i znawstwem kontynuował jego syn, Jan hr. Działyński, który pozostawił po sobie kolekcję liczącą około 1500 gatunków. Ostatnim właścicielem Kórnika był Władysław hr. Zamoyski, który przekazał dobra kórnickie narodowi polskiemu, powołując Fundację Zakłady Kórnickie. Na stanowisko pierwszego dyrektora Ogrodów Kórnickich powołany został Antoni Wróblewski, który przyczynił się do znakomitego poszerzenia kolekcji dendrologicznych, a także rozwinął dział szkółkarski. W 1933 r. utworzono pierwszy dział powstającego Zakładu Badania Drzew i Lasu, nazwany „Działem Dendrologii i Pomologii", który z czasem przekształcił się w Instytut Dendrologii Polskiej Akademii Nauk (Jagodziński 2023; Jagodziński i Biniaś-Szkopek 2024).

Aktualnie kolekcja Arboretum liczy około 3500 taksonów. Tak bogata kolekcja dendrologiczna stanowi doskonały obiekt do prowadzenia badań z zakresu porównywania cech roślin rosnących na odległych geograficznie obszarach dzięki układowi doświadczenia odpowiadającemu warunkom *common garden* (Paź-Dyderska i in. 2020). Zbliżone warunki środowiskowe panujące na terenie Arboretum sprawiają, że uzasadnione jest porównywanie cech funkcjonalnych roślin rosnących na jego obszarze (Roddy i in. 2019). Dzięki dużemu zróżnicowaniu taksonomicznemu posiadanych gatunków, Arboretum dostarcza także możliwości do wykonywania analiz z zakresu ich podobieństwa filogenetycznego. Długa historia Arboretum sprawia, że posiada ono w swojej kolekcji wiele okazów, które osiągnęły wiek dojrzały. Dzięki temu możliwe jest pozyskanie prób kwiatów i owoców wielu gatunków drzew i krzewów dojrzewających dopiero po wielu latach.

3.2. Zbiór danych

Zbiór danych do niniejszej rozprawy obejmował wyniki pomiarów różnych parametrów kwiatów, liści i owoców dla 79 gatunków roślin drzewiastych występujących na terenie Arboretum. Zbiór prowadziliśmy od marca 2021 r. do sierpnia 2022 r. Organy zbieraliśmy w momencie ich pełnego rozwoju, unikając kwiatów, liści i owoców uszkodzonych w wyniku działania czynników biotycznych (np. żerowanie owadów lub występowanie grzybów patogenicznych) bądź abiotycznych (np. susza lub grad). Z każdego osobnika pobraliśmy dwie próby kwiatów, liści i owoców – z najbardziej zacienionej (północnej) i najbardziej naświetlonej (południowej) części korony. Wyjątek stanowiła część okazów, z których nie pozyskaliśmy prób zawierających owoce. Wynika to z tego, iż w trakcie zbioru materiału część okazów w ogóle nie wytworzyła owoców m.in. w wyniku późnowiosennych przymrozków, a część owoców nie osiągnęła pełnej dojrzałości w wyniku żerowania ptaków lub została uszkodzona w wyniku suszy, silnych wiatrów bądź gradu. W rezultacie pozyskaliśmy po dwie próby: kwiatów dla 79 gatunków, liści dla 79 gatunków i owoców dla 33 gatunków, uzyskując łącznie 382 próby. Materiał pobieraliśmy przy pomocy sekatora na wysięgniku o długości 5 m. Każda próba składała się z 10 kwiatów, liści lub owoców, choć w przypadku ich niewielkich rozmiarów zwiększaliśmy wielkość próby, by zapewnić odpowiednią ilość materiału do analiz chemicznych. W przypadku znacznych rozmiarów kwiatów i owoców bądź ich niewielkiej dostępności, pobieraliśmy mniejszą ich liczbę, by nie uszkodzić cennych okazów (np. *Magnolia tripetala* o bardzo dużych, a niezbyt licznych kwiatach). Próby umieszczaliśmy w woreczkach strunowych i przechowywaliśmy w lodówce w temperaturze ok. 4°C przez maksymalnie 24 godziny.

Pomiary cech poszczególnych organów uwzględniały cechy morfologiczne oraz chemiczne. Cechy kwiatów obejmowały: długość i szerokość pojedynczego kwiatu (mm), zawartość węgla (C, %), zawartość azotu (N, %), stosunek C:N oraz suchą masę pojedynczego kwiatu (g). Ponadto, przeanalizowane zostały cztery cechy związane z zawartością cukrów i fenoli: określiliśmy procentową zawartość węglowodanów niestrukturalnych, węglowodanów rozpuszczalnych, skrobi oraz związków fenolowych. W przypadku owoców, pomiary obejmowały długość i średnicę owocu (mm), zawartość węgla (%), zawartość azotu (%), stosunek C:N oraz suchą masę (g). Pomiary liści objęły specyficzną powierzchnię liścia (ang. *specific leaf area*, SLA, $cm^2 g^{-1}$), zawartość węgla (%), zawartość azotu (%) oraz stosunek C:N.

Długość i szerokość kwiatów oraz długość i średnicę owoców mierzyliśmy za pomocą suwmiarek elektronicznych o dokładności 0,001 mm. Długość kwiatu mierzona była bez szypułki, od dna kwiatowego do najdalej wysuniętej części kwiatu, wzdłuż osi kwiatu. Szerokość kwiatu była mierzona prostopadle do osi, w której mierzona była długość kwiatu, w jego najszerszym miejscu. Podobnie długość owoców była mierzona bez szypułki, wzdłuż osi wyznaczanej przez szypułkę, a średnica owoców stanowiła wymiar mierzony prostopadle, w najszerszym miejscu owocu. Po dokonaniu pomiarów obliczyliśmy średnie wartości dla każdej próbki. Następnie próby suszyliśmy w suszarkach z wymuszonym obiegiem powietrza w temperaturze 65°C (ULE 600 i UF450, Memmert GmbH + Co. KG, Ratyzbona, Niemcy) do osiągnięcia stałej masy. Suchą masę określaliśmy używając wag o dokładności 0,001 g. Do skanowania liści użyliśmy oprogramowania WinFOLIA 2020 PRO (Regent Instruments Inc., Quebec, Kanada), mierząc ich powierzchnię z rozdzielczością 300 DPI. Następnie suszyliśmy liście do osiągnięcia stałej masy. Po wysuszeniu ważyliśmy próbki liści za pomocą wag o dokładności 0,001 g. SLA, obliczane jako stosunek powierzchni liścia do suchej masy liścia, wyznaczyliśmy na podstawie tych pomiarów. Po zważeniu materiał roślinny ze wszystkich prób zmieliliśmy.

Zawartość węgla i azotu w próbkach określiliśmy za pomocą Elementarnego Systemu Spalania ECS CHNS – O 4010 (Costech Instruments, Włochy/USA) i Analizatora CHNS/O Serii II 2400 (Perkin Elmer, USA). Zawartość sumy cukrów niestrukturalnych (ang. *total non-structural carbohydrates*, TNC), w tym cukrów rozpuszczalnych (ang. *soluble carbohydrates*, SC) i skrobi, określiliśmy zgodnie z metodyką zaproponowaną przez Hansena i Møllera (1975) oraz Haissiga i Dicksona (1979). Zawartość cukrów rozpuszczalnych mierzono po ich ekstrakcji w mieszaninie metanol-chloroform-woda, a pozostałość posłużyła do określenia zawartości skrobi. Zawartość sumy związków fenolowych (ang. *total phenolic compounds*, TPh) mierzyliśmy za pomocą odczynnika fenolowego Folina i Ciocalteu (SIGMA F-9252) zgodnie z metodologią Johnsona i Schaala (1957) z modyfikacją Singletona i Rossiego (1965).

3.3. Analizy statystyczne

Do analizy danych wykorzystaliśmy program R (R Core Team, 2023). Do przetwarzania danych użyliśmy pakietu *dplyr*, a do wizualizacji pakietu *ggplot2* (Wickham i in. 2020a, 2020b). Średnie wartości wszystkich zmierzonych cech zostały podane wraz z wartościami błędu standardowego (ang. *standard error*, SE). Aby określić zmienność badanych cech na poziomie międzygatunkowym, przeanalizowaliśmy różnice we współczynnikach zmienności (ang. *coefficient of variation*, CV), obliczanych jako odchylenie standardowe podzielone przez średnią między dwiema cechami, używając zmodyfikowanego testu współczynnika prawdopodobieństwa zaproponowanego przez Krishnamoorthy'ego i Lee (2014), czyli testu M-SLR, korzystając z funkcji *cvequality::mslr_test()* (Marwick i Krishnamoorthy 2019). Zdecydowaliśmy się na użycie testu M-SLR ze względu na niższe wskaźniki błędów typu I oraz zwiększoną moc w różnych warunkach w porównaniu do powszechnie stosowanego testu asymptotycznego Feltza i Millera (1996), zgodnie z sugestiami Funka (2008) i Paquette'a i in. (2012). Dodatkowo, test M-SLR uwzględnia nierówne liczby próbek, co było kluczowe w przypadku zebranego w ramach niniejszej rozprawy materiału badawczego. Aby uniknąć zwiększonego ryzyka błędów typu I przy przeprowadzaniu wielu testów hipotez (pary CV dla każdej cechy), zastosowaliśmy poprawkę Holma-Bonferroniego (Holm 1979). Analizy dotyczące zmienności międzygatunkowej opierały się na uśrednionych wartościach cech dla prób z nasłonecznionej i zacienionej części korony.

Aby określić poziom zmienności cech na poziomie wewnątrzosobniczym, użyliśmy wskaźnika plastyczności (ang. *plasticity index*, PI). Zgodnie z metodologią zaproponowaną przez Valladaresa i in. (2000), PI został obliczony przez określenie różnicy między maksymalną i minimalną wartością danej cechy, a następnie poprzez podzielenie jej przez maksymalną wartość cech. W naszych badaniach maksymalne i minimalne wartości uzyskano ze średnich wartości cech w dwóch próbkach, zebranych z nasłonecznionej i zacienionej części korony. W konsekwencji wyższa z dwóch wartości reprezentowała nasze maksimum, a niższa – minimum. Analizy dotyczące wewnątrzosobniczej zmienności cech obejmowały dwie próbki (jedną z każdego wariantu świetlnego, tj. z nasłonecznionej i zacienionej części korony). Użyliśmy PI dla każdego gatunku jako ustandaryzowanej miary wielkości efektu, niezależnej od wartości cech.

Aby ocenić wpływ wariantów świetlnych na wartości cech i ich PI wykorzystaliśmy test t-Studenta dla prób sparowanych, uwzględniający podobieństwo filogenetyczne pomiędzy gatunkami, używając funkcji *phyl.pairedttest* z pakietu *phytools* (Revell 2020). W tym teście porównaliśmy PI każdej pary cech, używając gatunków jako obserwacji. Test ten rozszerza tradycyjny test t-Studenta dla prób sparowanych, uwzględniając filogenetyczne podobieństwo obserwacji. Informacje o filogenetycznym podobieństwie gatunków uzyskaliśmy z drzewa filogenetycznego pobranego z pakietu *V.PhyloMaker2* (Jin i Qian 2022). Zawiera on megadrzewo dla szerokiego zakresu gatunków roślin z całego świata, bazujące na danych molekularnych, które jest docinane do zakresu danych zdefiniowanych przez użytkownika. W naszym przypadku było to 79 badanych gatunków. Po uzyskaniu docelowego drzewa filogenetycznego dokonaliśmy wizualnej inspekcji poprawności architektury gałęzi. Do określenia stopnia korelacji wartości oraz zmienności badanych cech z filogenezą gatunków wykorzystaliśmy wyżej opisane dane o filogenezie gatunków, a także obliczyliśmy wskaźniki K Blomberga oraz Λ Pagela używając pakietu *phylosignal* (Keck 2020).

Aby określić, w jakim stopniu zaproponowane przez nas cechy kwiatów i owoców korespondują z powszechnie wykorzystywanymi cechami z PES, pozyskaliśmy dane dla trzech cech, których pomiary nie były uwzględnione w naszych badaniach (tj. wysokość, masa nasion i gęstość drewna), z bazy danych TRY (Kattge i in. 2020). Ze względu na braki w bazie dotyczące wartości cech dla niektórych gatunków, zastosowaliśmy metodę imputacji danych, aby wypełnić luki. Metoda ta bazowała na analizie siły korelacji między cechami i między cechami a filogenezą gatunków, zgodnie z metodologią używaną m.in. w naszych wcześniejszych badaniach (Paź-Dyderska i Jagodziński 2023) oraz zgodnie z podejściem opisanym przez Pyška i in. (2015). Do imputacji użyliśmy znanych wartości cech i wektorów własnych filogenezy, uzyskanych z drzewa filogenetycznego za pomocą pakietu *PVR* (Santos, 2018). Te zmienne były używane w imputacjach opartych na lesie losowym z pakietu *missForest* (Stekhoven i Bühlmann 2012). Zdecydowaliśmy się wzmocnić moc predykcyjną za pomocą wektorów własnych filogenezy, ponieważ jak wykazali Penone i in. (2014), może to znacznie zwiększyć dokładność szacowania brakujących wartości cech. Przyjmując takie podejście, zapewniliśmy kompleksowy zestaw danych do analizy, zachowując integralność naszych badań pomimo braku wartości dla niektórych cech. Imputowaliśmy brakujące dane dotyczące cech kwiatów dla siedmiu gatunków (8,8%), cech owoców dla 46 gatunków (58,2%), wysokości dla 15 gatunków (19,0%), masy nasion dla 21 gatunków (26,6%) i gęstości pnia dla 49 gatunków (62,0%). Znormalizowana wartość pierwiastka średniego błędu kwadratowego (RMSE) imputacji wyniosła 0,50. Taka proporcja brakujących danych oraz wartość znormalizowanego RMSE nadal pozwalają na rzetelną analizę danych (Stewart i in. 2023).

Aby zbadać potencjalne związki między nowo proponowanymi cechami kwiatów i owoców a często wykorzystywanymi cechami z PES (Díaz i in. 2016), przeprowadziliśmy analizę głównych składowych (ang. *principal component analysis*, PCA) za pomocą pakietu *vegan* (Oksanen i in. 2022). Użycie PCA pozwoliło nam eksplorować powiązania między różnymi cechami i ocenić, czy nowe cechy reprezentują dodatkowe wymiary zmienności formy i funkcji roślin wśród badanych gatunków. Przed PCA standaryzowaliśmy wartości cech, odejmując średnią (tj. centrowanie) i dzieląc przez odchylenie standardowe (tj. skalowanie). Standaryzacja jest niezbędną procedurą umożliwiającą porównywanie zmiennych o różnym zakresie wartości, gdyż inaczej znaczenie cech o dużych wartościach byłoby przeszacowane w analizie. Oceniliśmy także wzajemne zależności dla każdej pary badanych cech przy pomocy analizy współczynników korelacji r Pearsona, skorygowanych o odległości filogenetyczne pomiędzy gatunkami. W tym celu wykorzystaliśmy metodę zaproponowaną przez Zhenga i in. (2009), używając funkcji *corphylo* z pakietu *ape* (Paradis i Schliep 2019).

4. Główne wyniki pracy

4.1. Stopień korelacji cech reprodukcyjnych i ich zmienności z filogenezą

Publikacja 1. *Low intra-canopy variability of floral traits in temperate woody plants.*
Analizując cechy kwiatów 79 gatunków drzew i krzewów wykryliśmy statystycznie istotne sygnały filogenetyczne dla wszystkich sześciu badanych cech kwiatów: długości i szerokości kwiatu, suchej masy, zawartości C i N oraz stosunku C:N. Współczynniki K Blomberga i Λ Pagela jednoznacznie wskazały, że najsilniejszy sygnał ewolucyjny wystąpił w przypadku suchej masy kwiatu, a następnie – długości kwiatu. Najsłabszy, ale nadal statystycznie istotny sygnał filogenetyczny, zaobserwowaliśmy w stosunku C:N.

Publikacja 2. *Intra- and Interspecific Variability of Non-Structural Carbohydrates and Phenolic Compounds in Flowers of 70 Temperate Trees and Shrubs.*
Wyniki analiz wykazały obecność sygnału filogenetycznego dla dwóch z czterech analizowanych cech dotyczących zawartości związków chemicznych w kwiatach. Analizy te miały na celu określenie, czy międzygatunkowa zmienność zawartości poszczególnych związków jest powiązana z historią ewolucyjną gatunków. Zaobserwowaliśmy występowanie sygnału filogenetycznego dla skrobi i TPh. Zawartość skrobi wykazała najsilniejszy sygnał filogenetyczny, jednak głównie z powodu wartości odstającej dla *Paulownia tomentosa*, przez co nie był to wynik statystycznie istotny. W przypadku TPh zaobserwowaliśmy umiarkowany, ale istotny statystycznie sygnał filogenetyczny. Nie odnotowaliśmy natomiast korelacji między historią ewolucyjną gatunków a zawartością węglowodanów rozpuszczalnych czy TNC.

4.2. Porównanie zmienności cech reprodukcyjnych na poziomie wewnątrzosobniczym i międzygatunkowym

Publikacja 1. *Low intra-canopy variability of floral traits in temperate woody plants.*
Zawartość węgla w kwiatach badanych gatunków wynosiła od 40,91% (*Euonymus atropurpureus*) do 47,41% (*Viburnum sieboldii*), ze średnią 44,42% ± 0,16. Cecha ta miała najniższy współczynnik zmienności (CV) spośród badanych (3,09%). Zawartość azotu

w kwiatach wynosiła od 1,29% (*Castanea sativa*) do 5,22% (*Sambucus kamtschatica*), ze średnią 2,97% ± 0,11 i CV równym 31,21%. Najniższy stosunek C:N stwierdzono dla *Calycanthus floridus* var. *glaucus* (9,81), a najwyższy dla *Castanea sativa* (40,58), ze średnią 19,43% ± 0,74 i CV wynoszącym 32,41%. Długość kwiatu wynosiła od 0,68 mm (*Salix gracilistyla*) do 155,68 mm (*Davidia involucrata*), a szerokość od 0,61 mm (*Salix gracilistyla*) do 122,61 mm (*Magnolia tripetala*). Średnia długość kwiatów wynosiła 20,65 ± 2,72 mm i CV wynoszącym 117,19%, a średnia szerokość to 20,19 ± 2,21 mm, przy CV równym 97,44%. Sucha masa pojedynczego kwiatu wynosiła od 0,0001 g (*Salix gracilistyla*) do 9,1655 g (*Magnolia tripetala*), ze średnią 0,2414 ± 0,1182 g i z najwyższym CV wśród badanych cech (435,14%).

W przypadku analizy zmienności wewnątrzosobniczej stwierdziliśmy istotne statystycznie różnice między próbami z dwóch wariantów świetlnych jedynie dla zawartości azotu w kwiatach i stosunku C:N. Średnie różnice dla tych cech pomiędzy wariantami świetlnymi, czyli między próbami z nasłonecznionej i zacienionej części korony, skorygowane o podobieństwo filogenetyczne, wyniosły odpowiednio 0,1611 (95% CI: 0,0390 do 0,2832) i -1,1832 (95% CI: -2,1502 do -0,02136). Pozostałe cechy nie wykazały istotnych statystycznie różnic pomiędzy próbami reprezentującymi nasłonecznione i zacienione części koron. Minimalne różnice w ramach gatunku pomiędzy badanymi częściami korony w zawartości węgla i azotu w kwiatach wynosiły 0,01% (*Prunus padus* i *Cydonia oblonga*), 0,02 dla stosunku C:N (*Torminalis glaberrima*), 0,05 mm dla długości (*Hamamelis virginiana*), 0,02 mm dla szerokości (*Aesculus parviflora*) oraz <0,001 g dla suchej masy kwiatów (np. *Staphylea colchica*). Maksymalne różnice to 1,90% dla zawartości C (*Asimina triloba*), 2,26% dla zawartości N (*Aesculus turbinata*), 18,27 dla stosunku C:N (*Paulownia tomentosa*), 58,45 mm dla długości (*Malus ×hartwigii*), 82,45 mm dla szerokości (*Malus ×hartwigii*) i 5,42 g dla suchej masy kwiatów (*Malus ×hartwigii*).

Publikacja 2. *Intra- and Interspecific Variability of Non-Structural Carbohydrates and Phenolic Compounds in Flowers of 70 Temperate Trees and Shrubs.*

Średnia zawartość rozpuszczalnych węglowodanów w kwiatach badanych gatunków wynosiła od 3,2% (*Ailanthus altissima*) do 27,1% (*Catalpa bignonioides*), ze współczynnikiem zmienności (CV) równym 44,4%. Średnia zawartość skrobi wynosiła od 0,7% (*Viburnum sieboldii*) do 10,3% (*Asimina triloba*), a CV wyniósł 110,4%. Średnie wartości TNC wynosiły od 4,0% (*Ailanthus altissima*) do 27,8% (*Catalpa bignonioides*), z CV równym 41,4%. Wartości TPh wynosiły od 46,1 µg g^{-1} kwasu chlorogenowego (*Laburnum anagyroides*) do 1085,7 µg g^{-1} (*Sorbus torminalis*), przy CV wynoszącym 70,5%. Zmienność badanych cech była najwyższa w przypadku zawartości skrobi, a najniższa dla zawartości rozpuszczalnych węglowodanów i TNC.

Nie zaobserwowaliśmy statystycznie istotnych różnic ani biologicznie znaczących różnic między częściami korony o wysokim i niskim nasłonecznieniu. Średnie różnice dla tych cech pomiędzy wariantami dla rozpuszczalnych węglowodanów, skrobi, TNC i TPh wyniosły odpowiednio -1,0%, 0,4%, -0,8% i 51,1 µg g^{-1}. Minimalne różnice wyniosły: 0,2% dla rozpuszczalnych węglowodanów (*Halesia carolina*), <0,01% dla skrobi (np. *Castanea sativa*), 0,2% dla TNC (*Paulownia tomentosa*) i 0,5 µg kwasu chlorogenowego na gram suchej masy dla TPh (*Tilia cordata*). Maksymalne różnice wyniosły: 28,8% dla rozpuszczalnych węglowodanów (*Spiraea nudiflora*), 7,0% dla skrobi (*Zelkova serrata*), 29,0% dla TNC (*Spiraea nudiflora*) i 1021,8 µg kwasu chlorogenowego na gram suchej masy dla TPh (*Spiraea longigemmis*).

Publikacja 3. *Potential of reproductive traits in functional ecology: A quantitative comparison of variability in floral, fruit, and leaf traits.*

Wśród badanych cech, te związane z suchą masą kwiatów i owoców wykazały najwyższą zmienność międzygatunkową, natomiast cechy związane z zawartością węgla w kwiatach i liściach miały najniższą zmienność. Sucha masa kwiatów miała najwyższy współczynnik zmienności (CV = 435,1%). Kolejne pod względem CV były sucha masa owoców (CV = 251,0%) oraz zawartość azotu w owocach (CV = 241,9%). Cechy związane z zawartością węgla były najmniej zmienne. Cechy opisujące rozmiar badanych organów, takie jak długość i szerokość kwiatów oraz długość i średnica owoców, wykazywały umiarkowany zakres zmienności. SLA miała ograniczony poziom zmienności międzygatunkowej (CV = 36,9%), co umiejscawia ją poniżej cech związanych z suchą masą kwiatów i owoców oraz cech rozmiarowych (CV długości kwiatów = 117,2%; szerokości kwiatów = 97,4%; długości owoców = 84,4%; średnicy owoców = 76,7%).

Wśród badanych cech, SLA wykazała najwyższą zmienność wewnątrzosobniczą, ze średnim PI wynoszącym 30,0%. Na kolejnych miejscach uplasowały się sucha masa kwiatów (PI = 17,5%) i owoców (PI = 15,2%). Cechy związane z zawartością węgla w organach miały najmniejszą zmienność, z najmniejszą zmiennością dla zawartości węgla w kwiatach (PI = 1,3%). Cechy związane z zawartością azotu wykazywały pośrednią zmienność wewnątrzosobniczą (PI dla kwiatów, owoców i liści wyniosły odpowiednio 11,3%, 12,6% i 11,1%). Cechy rozmiarowe miały wartości PI na poziomie 9,2% dla długości kwiatów, 10,3% dla szerokości kwiatów, 6,4% dla długości owoców i 5,9% dla średnicy owoców.

4.3. Porównanie wewnątrzosobniczej zmienności cech reprodukcyjnych względem cech bardziej zależnych od dostępności zasobów (*performance-related traits*)

Publikacja 3. *Potential of reproductive traits in functional ecology: A quantitative comparison of variability in floral, fruit, and leaf traits.*

W wizualizacji porównawczej średniej zmienności międzygatunkowej i wewnątrzosobniczej zauważyliśmy różnice zarówno w średnich wartościach zmienności, jak i w ich zakresach. Cechy dotyczące zawartości węgla w analizowanych organach wykazywały najmniejszą zmienność, zarówno międzygatunkową, jak i wewnątrzosobniczą. Cechy związane z rozmiarem oraz z zawartością azotu miały wartości pośrednie CV oraz PI. Sucha masa kwiatów charakteryzowała się najwyższym zakresem wartości zmienności międzygatunkowej oraz ograniczonym zakresem zmienności wewnątrzosobniczej. Warto zauważyć, że SLA miała szczególnie wysokie średnie wartości PI i szeroki zakres wartości, podczas gdy jej zmienność międzygatunkowa była stosunkowo niska.

4.4. Zależności pomiędzy cechami reprodukcyjnymi a powszechnie wykorzystywanymi cechami reprezentującymi globalne spektrum form i funkcji roślin

Publikacja 3. *Potential of reproductive traits in functional ecology: A quantitative comparison of variability in floral, fruit, and leaf traits.*

Analiza PCA ujawniła główne kierunki zmienności badanych cech funkcjonalnych. Oś PC1 wyjaśniała 21,54% zmienności, a oś PC2 – 15,22%. Wartości ujemne na osi PC1 były związane z wyższymi wartościami trzech cech zaproponowanych przez Díaz i in. (2016): powierzchni liścia, wysokości oraz masy nasion, a także z wyższymi wartościami cech dotyczących masy i rozmiaru kwiatów oraz owoców. Wartości dodatnie na osi PC1 były skorelowane z gęstością drewna, która zwiększała się wraz z wartością współrzędnej PC1. Wzrost wartości na osi PC2 korelował z wyższą koncentracją azotu we wszystkich analizowanych organach oraz większym SLA. Z kolei oś PC2 wykazywała negatywną korelację z zawartością węgla i stosunkiem C:N, niezależnie od badanego organu. Żadna z mierzonych cech nie ujawniła odrębnego wymiaru zmienności w przestrzeni cech. Analiza wzajemnych korelacji poszczególnych cech wykazała najsilniejsze zależności między cechami dotyczącymi rozmiarów organów, a także w przypadku cech związanych z zawartością azotu w różnych organach. Masa nasion była pozytywnie skorelowana z wymiarami owoców i ich suchą masą oraz maksymalną wysokością drzewa.

5. Podsumowanie i wnioski

Wyniki uzyskane w ramach realizacji niniejszej pracy doktorskiej uzupełniają wiedzę na temat dynamicznie rozwijającej się gałęzi ekologii, jaką jest ekologia funkcjonalna. Nowa wiedza dotyczy wartości cech kwiatów i owoców oraz poziomu ich zmienności, a także potencjału tych cech w zakresie dalszego wykorzystania w badaniach strategii życiowych gatunków drzewiastych. Dzięki określeniu związków badanych cech z filogenezą oraz analizie relacji cech kwiatów i owoców z lepiej reprezentowanymi w bazach danych cechami pozostałych organów roślin, możliwe jest ekstrapolowanie wyników na inne gatunki drzew strefy klimatu umiarkowanego. Pozwoli to na dalsze wykorzystanie uzyskanych wyników w badaniach różnorodności biologicznej i przemian ekosystemów. W wyniku przeprowadzonych badań stwierdzono, że:

- Istnieje znaczna zmienność badanych cech kwiatów i owoców na poziomie międzygatunkowym, co wynika z szerokiego spektrum strategii reprodukcyjnych badanych gatunków.
- Istnieje istotna statystycznie korelacja między cechami kwiatów dotyczącymi ich rozmiaru (długość i szerokość kwiatu oraz jego sucha masa) a historią ewolucyjną gatunków. Podobnie jest w przypadku zawartości węgla i azotu oraz stosunku C:N w kwiatach.
- W przypadku wewnątrzosobniczej zmienności cech kwiatów dotyczących zawartości cukrów i fenoli, sygnał filogenetyczny odnotowano jedynie w przypadku zawartości skrobi i związków fenolowych.
- Dostępność światła ma niewielki wpływ na zmienność badanych cech kwiatów i owoców na poziomie wewnątrzosobniczym.
- Stosunek zmienności wewnątrzosobniczej do międzygatunkowej jest zależny od specyfiki danej cechy, natomiast cechą o największej wśród badanych zmienności

międzygatunkowej była sucha masa kwiatu, a o największej zmienności wewnątrzosobniczej – specyficzna powierzchnia liścia.

- Analizowane cechy kwiatów i owoców uzupełniają globalne spektrum form i funkcji roślin i są zgodne z wykorzystywanymi do tej pory cechami pozostałych organów. Przykładowo, nasze wyniki sugerują, że gatunki o dużej powierzchni liści i masie nasion prawdopodobnie mają kwiaty i owoce o większej suchej masie i większych rozmiarach. Warto zauważyć, że cechy związane z rozmiarem kwiatów i owoców wykazywały znaczne nakładanie się, co sugeruje potencjalną korelację między rozmiarami tych organów.

Wyniki przeprowadzonych badań jednoznacznie wskazują na znaczny potencjał cech kwiatów i owoców w dalszych badaniach z zakresu ekologii funkcjonalnej. Korelacje z filogenezą, a także duża zmienność międzygatunkowa przy jednoczesnej dużej stabilności cech na poziomie wewnątrzosobniczym pozwalają sugerować, że ekstrapolacja pomiarów tych cech na pozostałe osobniki danego gatunku w przypadku wielu rodzajów badań ekologicznych jest uzasadniona. Duża zgodność cech kwiatów i owoców z powszechnie wykorzystywanymi cechami pozostałych organów zachęca do podjęcia dalszych badań, mających na celu pełne zrozumienie różnorodności form oraz sposobów funkcjonowania gatunków, ze szczególnym uwzględnieniem ich strategii reprodukcyjnych.

6. Literatura

Anderson B., Johnson S.D. 2009. Geographical covariation and local convergence of flower depth in a guild of fly-pollinated plants. New Phytologist 182, 533–540. https://doi.org/10.1111/j.1469-8137.2009.02764.x

Aubin I., Munson A.D., Cardou F., Burton P.J., Isabel N., Pedlar J.H. i in. 2016. Traits to stay, traits to move: a review of functional traits to assess sensitivity and adaptive capacity of temperate and boreal trees to climate change. Environmental Reviews 24, 164–186. https://doi.org/10.1139/er-2015-0072

Bentos T.V., Mesquita R.C.G., Camargo J.L.C., Williamson G.B. 2014. Seed and fruit tradeoffs – the economics of seed packaging in Amazon pioneers. Plant Ecology & Diversity 7, 371–382. https://doi.org/10.1080/17550874.2012.740081

Bernhardt P. 2000. Convergent Evolution and Adaptive Radiation of Beetle-Pollinated Angiosperms. W: Dafni A., Hesse M., Pacini E. (red.). Pollen and Pollination. Springer, Wiedeń. Ss. 293–320. https://doi.org/10.1007/978-3-7091-6306-1_16

Białobok S. 1955. Rys historyczny Zakładu Dendrologii i Pomologii w Kórniku oraz ogólna charakterystyka kolekcji drzew i krzewów. Arboretum Kórnickie l, 7–30.

Bussotti F., Pollastrini M., Holland V., Brüggemann W. 2015. Functional traits and adaptive capacity of European forests to climate change. Environmental and Experimental Botany 111, 91–113. https://doi.org/10.1016/j.envexpbot.2014.11.006

Díaz S., Kattge J., Cornelissen J.H.C., Wright I.J., Lavorel S., Dray S. i in. 2016. The global spectrum of plant form and function. Nature 529, 167–171. https://doi.org/10.1038/nature16489

E-Vojtkó A., de Bello F., Durka W., Kühn I., Götzenberger L. 2020. The neglected importance of floral traits in trait-based plant community assembly. Journal of Vegetation Science 31, 529–539. https://doi.org/10.1111/jvs.12877

E-Vojtkó A., Junker R.R., de Bello F., Götzenberger L. 2022. Floral and reproductive traits are an independent dimension within the plant economic spectrum of temperate central Europe. New Phytologist 236, 1964–1975. https://doi.org/10.1111/nph.18386

Feltz C.J., Miller G.E. 1996. An asymptotic test for the equality of coefficients of variation from k populations. Statistics in Medicine 15, 647–658. https://doi.org/10.1002/(SICI)1097-0258(19960330)15:6<647::AID-SIM184>3.0.CO;2-P

Feng F., Li M., Ma F., Cheng L. 2014. Effects of location within the tree canopy on carbohydrates, organic acids, amino acids and phenolic compounds in the fruit peel and flesh from three apple (*Malus ×domestica*) cultivars. Horticulture Research 1, 14019. https://doi.org/10.1038/hortres.2014.19

Funk J.L. 2008. Differences in plasticity between invasive and native plants from a low resource environment. Journal of Ecology 96, 1162–1173. https://doi.org/10.1111/j.1365-2745.2008.01435.x

Haissig B.E., Dickson R.E. 1979. Starch Measurement in Plant Tissue Using Enzymatic Hydrolysis. Physiologia Plantarum 47, 151–157. https://doi.org/10.1111/j.1399-3054.1979.tb03207.x

Hansen J., Møller I. 1975. Percolation of starch and soluble carbohydrates from plant tissue for quantitative determination with anthrone. Analytical Biochemistry 68, 87–94. https://doi.org/10.1016/0003-2697(75)90682-X

Holm S. 1979. A Simple Sequentially Rejective Multiple Test Procedure. Scandinavian Journal of Statistics 6, 65–70.

Jagodziński A.M. 2023. Instytut Dendrologii PAN – czerpiąc z historii, tworząc przyszłość. W: Tomaszewski D., Jagodziński A.M. (red.) 2023. Biologia i ekologia roślin drzewiastych. Konferencja naukowa połączona z obchodami Jubileuszu 90-lecia Instytutu Dendrologii PAN w Kórniku. Kórnik-Poznań, 9–11 października 2023 roku. Materiały konferencyjne. Bogucki Wydawnictwo Naukowe, Poznań. Ss. 23–46.

Jagodziński A.M., Biniaś-Szkopek M. 2024. Władysław hr. Zamoyski – nasz Fundator. Kórniczanin 1, 16–17.

Jagodziński A.M., Nowak-Dyjeta K. 2012. Przyrodniczy pomnik historii. Arboretum Kórnickie. Las Polski 12, 18–19.

Jin Y., Qian H. 2022. V.PhyloMaker2: An updated and enlarged R package that can generate very large phylogenies for vascular plants. Plant Diversity 44, 335–339. https://doi.org/10.1016/j.pld.2022.05.005

Johnson G., Schaal L.A. 1957. Accumulation of phenolic substances and ascorbic acid in potato tuber tissue upon injury and their possible role in disease resistance. American Potato Journal 34, 200–209. https://doi.org/10.1007/BF02854948

Kąsinowska R. 2019. Zamek w Kórniku. Polska Akademia Nauk. Zakład Poligraficzny Moś i Łuczak sp. j., Poznań.

Kattge J., Bönisch G., Díaz S., Lavorel S., Prentice I.C., Leadley P. i in. 2020. TRY plant trait database – enhanced coverage and open access. Global Change Biology 26, 119–188. https://doi.org/10.1111/gcb.14904

Keck F. 2020. Phylosignal: Exploring the Phylogenetic Signal in Continuous Traits. URL: https://cran.r-project.org/package=phylosignal (Dostęp: 16.08.2024).

Kleyer M., Minden V. 2015. Why functional ecology should consider all plant organs: An allocation-based perspective. Basic and Applied Ecology 16, 1–9. https://doi.org/10.1016/j.baae.2014.11.002

Krishnamoorthy K., Lee M. 2014. Improved tests for the equality of normal coefficients of variation. Computational Statistics 29, 215–232. https://doi.org/10.1007/s00180-013-0445-2

Kühn N., Tovar C., Carretero J., Vandvik V., Enquist B.J., Willis K.J. 2021. Globally important plant functional traits for coping with climate change. Frontiers of Biogeography 13 (4), e53774. https://doi.org/10.21425/F5FBG53774

Kuppler J., Albert C.H., Ames G.M., Armbruster W.S., Boenisch G., Boucher F.C. i in. 2020. Global gradients in intraspecific variation in vegetative and floral traits are partially associated with climate and species richness. Global Ecology and Biogeography 29, 992–1007. https://doi.org/10.1111/geb.13077

Lanuza J.B., Rader R., Stavert J., Kendall L.K., Saunders M.E., Bartomeus I. 2023. Covariation among reproductive traits in flowering plants shapes their interactions with pollinators. Functional Ecology 37, 2072–2084. https://doi.org/10.1111/1365-2435.14340

Martin A.R., Doraisami M., Thomas S.C. 2018. Global patterns in wood carbon concentration across the world's trees and forests. Nature Geosciences 11, 915–920. https://doi.org/10.1038/s41561-018-0246-x

Marwick B., Krishnamoorthy K. 2019. cvequality: Tests for the Equality of Coefficients of Variation from Multiple Groups. URL: https://cran.r-project.org/package=cvequality (Dostęp: 16.08.2024).

Mouillot D., Graham N.A.J., Villéger S., Mason N.W.H., Bellwood D.R. 2013. A functional approach reveals community responses to disturbances. Trends in Ecology & Evolution 28, 167–177. https://doi.org/10.1016/j.tree.2012.10.004

Nowak K. 2020. Najstarsze drzewa Arboretum Kórnickiego: zarys historii kolekcji dendrologicznej na trzech planach parku. Rocznik Polskiego Towarzystwa Dendrologicznego 68, 63–76.

Nowak-Dyjeta K., Broniewska K., Bojarczuk T., Giertych M., Sękiewicz M. 2013. Arboretum Kórnickie – spotkanie z przyrodą. Przewodnik. Instytut Dendrologii Polskiej Akademii Nauk. Betmor Poligrafia s.c., Kórnik.

Oksanen J., Simpson G.L., Blanchet F.G., Kindt R., Legendre P., Minchin P.R. i in. 2022. vegan: Community Ecology Package. URL: https://cran.r-project.org/package=vegan (Dostęp: 16.08.2024).

Paquette A., Fontaine B., Berninger F., Dubois K., Lechowicz M.J., Messier C. i in. 2012. Norway maple displays greater seasonal growth and phenotypic plasticity to light than native sugar maple. Tree Physiology 32, 1339–1347. https://doi.org/10.1093/treephys/tps092

Paradis E., Schliep K. 2019. ape 5.0: an environment for modern phylogenetics and evolutionary analyses in R. Bioinformatics 35, 526–528. https://doi.org/10.1093/bioinformatics/bty633

Paź-Dyderska S., Dyderski M.K., Nowak K., Jagodziński A.M. 2020. On the sunny side of the crown – quantification of intra-canopy SLA variation among 179 taxa. Forest Ecology and Management 472, 118254. https://doi.org/10.1016/j.foreco.2020.118254

Paź-Dyderska S., Jagodziński A.M. 2023. In search of a perfect trait set: A workflow presentation based on the conservation status assessment of Poland's dendroflora. Ecology and Evolution 13, e9979. https://doi.org/10.1002/ece3.9979

Penone C., Davidson A.D., Shoemaker K.T., Marco M.D., Rondinini C., Brooks T.M. i in. 2014. Imputation of missing data in life-history trait datasets: which approach performs the best? Methods in Ecology and Evolution 5, 961–970. https://doi.org/10.1111/2041-210X.12232

Pyšek P., Manceur A.M., Alba C., McGregor K.F., Pergl J., Štajerová K. i in. 2015. Naturalization of central European plants in North America: species traits, habitats, propagule pressure, residence time. Ecology 96, 762–774. https://doi.org/10.1890/14-1005.1

R Core Team 2023. R: A language and environment for statistical computing. URL: https://www.r-project.org/ (Dostęp: 16.08.2024).

Reich P.B. 2014. The world-wide ‘fast–slow’ plant economics spectrum: a traits manifesto. Journal of Ecology 102, 275–301. https://doi.org/10.1111/1365-2745.12211

Revell L.J. 2020. phytools: Phylogenetic Tools for Comparative Biology (and Other Things). URL: https://cran.r-project.org/package=phytools (Dostęp: 16.08.2024).

Roddy A.B., Jiang G.-F., Cao K., Simonin K.A., Brodersen C.R. 2019. Hydraulic traits are more diverse in flowers than in leaves. New Phytologist 223, 193–203. https://doi.org/10.1111/nph.15749

Roddy A.B., Martínez-Perez C., Teixido A.L., Cornelissen T.G., Olson M.E., Oliveira R.S. i in. 2021. Towards the flower economics spectrum. New Phytologist 229, 665–672. https://doi.org/10.1111/nph.16823

Santos T. 2018. Phylogenetic Eigenvectors Regression and Phylogenetic Signal-Representation Curve. URL: https://cran.r-project.org/package=PVR (Dostęp: 16.08.2024).

Singleton V.L., Rossi J.A. 1965. Colorimetry of Total Phenolics with Phosphomolybdic-Phosphotungstic Acid Reagents. American Journal of Enology and Viticulture 16, 144–158.

Stekhoven D.J., Bühlmann P. 2012. MissForest - nonparametric missing value imputation for mixed-type data. Bioinformatics 28, 112–118. https://doi.org/10.1093/bioinformatics/btr597

Stewart K., Carmona C.P., Clements C., Venditti C., Tobias J.A., González-Suárez M. 2023. Functional diversity metrics can perform well with highly incomplete data sets. Methods in Ecology and Evolution 14, 2856–2872. https://doi.org/10.1111/2041-210X.14202

Streit R.P., Bellwood D.R. 2023. To harness traits for ecology, let’s abandon ‘functionality’. Trends in Ecology & Evolution 38, 402–411. https://doi.org/10.1016/j.tree.2022.11.009

Valladares F., Wright S.J., Lasso E., Kitajima K., Pearcy R.W. 2000. Plastic Phenotypic Response to Light of 16 Congeneric Shrubs from a Panamanian Rainforest. Ecology 81, 1925–1936. https://doi.org/10.1890/0012-9658(2000)081[1925:PPRTLO]2.0.CO;2

Wickham H., Chang W., Henry L., Pedersen T.L., Takahashi K., Wilke C. i in. 2020a. ggplot2: Create Elegant Data Visualisations Using the Grammar of Graphics. URL: https://cran.r-project.org/package=ggplot2 (Dostęp: 16.08.2024).

Wickham H., Francois R., Henry L., Müller K. 2020b. dplyr: A Grammar of Data Manipulation. URL: https://cran.r-project.org/package=dplyr (Dostęp: 16.08.2024).

Wright I.J., Reich P.B., Westoby M., Ackerly D.D., Baruch Z., Bongers F. i in. 2004. The worldwide leaf economics spectrum. Nature 428, 821. https://doi.org/10.1038/nature02403

Zhang C., Li J., Willis C.G., Ma Z. 2020. Among-population variation in seed mass for 190 Tibetan plant species: Phylogenetic pattern and ecological correlates. Global Ecology and Conservation 23, e01163. https://doi.org/10.1016/j.gecco.2020.e01163

Zheng L., Ives A.R., Garland T., Larget B.R., Yu Y., Cao K. 2009. New multivariate tests for phylogenetic signal and trait correlations applied to ecophysiological phenotypes of nine *Manglietia* species. Functional Ecology 23, 1059–1069. https://doi.org/10.1111/j.1365-2435.2009.01596.x

Oświadczenia

Oświadczenie kierującego pracą

Oświadczam, że niniejsza praca została przygotowana pod moim kierunkiem i stwierdzam, że spełnia ona warunki do przedstawienia jej w postępowaniu o nadanie stopnia doktora nauk biologicznych.

Kórnik, 10 września 2024 r. ....

podpis

Oświadczenie autorki pracy

Świadoma odpowiedzialności prawnej oświadczam, że niniejsza rozprawa doktorska została napisana przeze mnie samodzielnie i nie zawiera treści uzyskanych w sposób niezgodny z obowiązującymi przepisami.

Oświadczam również, że przedstawiona praca nie była wcześniej przedmiotem procedur związanych z uzyskaniem stopnia doktora w innej jednostce.

Oświadczam ponadto, że niniejsza wersja pracy jest identyczna z załączoną wersją elektroniczną.

……………………………………

Kórnik, 10 września 2024 r. podpis

mgr inż. Sonia Paź-Dyderska Kórnik, 10 września 2024 r.

Instytut Dendrologii Polskiej Akademii Nauk

Zakład Ekologii

OŚWIADCZENIE

Oświadczam, że w pracy:

Paź-Dyderska S., Jagodziński A.M. 2024. Low intra-canopy variability of floral traits in temperate woody plants. Global Ecology and Conservation 54, e03054. https://doi.org/10.1016/j.gecco.2024.e03054

Mój wkład w powstanie tej pracy polegał na udziale w opracowaniu koncepcji i metodyki badań, przeglądzie literatury związanej z analizowanym zagadnieniem, zbiorze danych w terenie, opracowaniu wyników i ich analizie statystycznej oraz na przygotowaniu manuskryptu pracy i wykonaniu korekty manuskryptu artykułu wg uzyskanych recenzji; pełniłam również rolę autorki korespondencyjnej. **Mój udział procentowy szacuję na 90%.**

Paź-Dyderska S., Żytkowiak R., Jagodziński A.M. 2022. Intra- and Interspecific Variability of Non-Structural Carbohydrates and Phenolic Compounds in Flowers of 70 Temperate Trees and Shrubs. Forests 13, 1256. https://doi.org/10.3390/f13081256

Mój wkład w powstanie tej pracy polegał na udziale w opracowaniu koncepcji i metodyki badań, przeglądzie literatury związanej z analizowanym zagadnieniem, zbiorze danych w terenie, opracowaniu wyników i ich analizie statystycznej oraz na przygotowaniu manuskryptu pracy i wykonaniu korekty manuskryptu artykułu wg uzyskanych recenzji; pełniłam również rolę autorki korespondencyjnej. **Mój udział procentowy szacuję na 80%.**

Paź-Dyderska S., Jagodziński A.M. 2024. Potential of reproductive traits in functional ecology: A quantitative comparison of variability in floral, fruit, and leaf traits. Ecology and Evolution 14, e11690. https://doi.org/10.1002/ece3.11690

Mój wkład w powstanie tej pracy polegał na udziale w opracowaniu koncepcji i metodyki badań, przeglądzie literatury związanej z analizowanym zagadnieniem, zbiorze danych w terenie, opracowaniu wyników i ich analizie statystycznej oraz na przygotowaniu manuskryptu pracy i wykonaniu korekty manuskryptu artykułu wg uzyskanych recenzji; pełniłam również rolę autorki korespondencyjnej. **Mój udział procentowy szacuję na 90%.**

………………………………………

podpis

prof. dr hab. inż. Andrzej M. Jagodziński Kórnik, 10 września 2024 r.

Instytut Dendrologii Polskiej Akademii Nauk

Zakład Ekologii

OŚWIADCZENIE

Oświadczam, że w pracy:

Paź-Dyderska S., **Jagodziński A.M.** 2024. Low intra-canopy variability of floral traits in temperate woody plants. Global Ecology and Conservation 54, e03054. https://doi.org/10.1016/j.gecco.2024.e03054

Mój wkład w powstanie tej pracy polegał na udziale w opracowaniu koncepcji i metodyki badań, udziale w interpretacji uzyskanych wyników, udziale w przygotowaniu manuskryptu artykułu i odpowiedzi na recenzje. **Mój udział procentowy szacuję na 10%.**

Paź-Dyderska S., Żytkowiak R., **Jagodziński A.M.** 2022. Intra- and Interspecific Variability of Non-Structural Carbohydrates and Phenolic Compounds in Flowers of 70 Temperate Trees and Shrubs. Forests 13, 1256. https://doi.org/10.3390/f13081256

Mój wkład w powstanie tej pracy polegał na udziale w opracowaniu koncepcji i metodyki badań, udziale w interpretacji uzyskanych wyników, udziale w przygotowaniu manuskryptu artykułu i odpowiedzi na recenzje. **Mój udział procentowy szacuję na 10%.**

Paź-Dyderska S., **Jagodziński A.M.** 2024. Potential of reproductive traits in functional ecology: A quantitative comparison of variability in floral, fruit, and leaf traits. Ecology and Evolution 14, e11690. https://doi.org/10.1002/ece3.11690

Mój wkład w powstanie tej pracy polegał na udziale w opracowaniu koncepcji i metodyki badań, udziale w interpretacji uzyskanych wyników, udziale w przygotowaniu manuskryptu artykułu i odpowiedzi na recenzje. **Mój udział procentowy szacuję na 10%.**

……………………………………

podpis

dr inż. Roma Żytkowiak Kórnik, 10 września 2024 r.

Instytut Dendrologii Polskiej Akademii Nauk

Zakład Ekologii

OŚWIADCZENIE

Oświadczam, że w pracy:

Paź-Dyderska S., **Żytkowiak R.**, Jagodziński A.M. 2022. Intra- and Interspecific Variability of Non-Structural Carbohydrates and Phenolic Compounds in Flowers of 70 Temperate Trees and Shrubs. Forests 13, 1256. https://doi.org/10.3390/f13081256

Mój wkład w powstanie tej pracy polegał na udziale w interpretacji uzyskanych wyników, przeprowadzeniu analiz chemicznych, udziale w przygotowaniu manuskryptu artykułu i odpowiedzi na recenzje. **Mój udział procentowy szacuję na 10%.**

....

podpis

Załączniki

Publikacja 1.

Paź-Dyderska S., Jagodziński A.M. 2024. Low intra-canopy variability of floral traits in temperate woody plants. Global Ecology and Conservation 54, e03054. https://doi.org/10.1016/j.gecco.2024.e03054

Impact Factor 5-letni (2023): 4,1

Punktacja MNiSW (2024): 100

Global Ecology and Conservation 54 (2024) e03054

Contents lists available at ScienceDirect

Global Ecology and Conservation

journal homepage: www.elsevier.com/locate/gecco

Low intra-canopy variability of floral traits in temperate woody plants

Sonia Paź-Dyderska [a,*], Andrzej M. Jagodziński [a,b]

[a] Institute of Dendrology, Polish Academy of Sciences, Parkowa 5, Kórnik 62-035, Poland
[b] Poznań University of Life Sciences, Faculty of Forestry and Wood Technology, Department of Game Management and Forest Protection, Wojska Polskiego 71c, Poznań 60-625, Poland

ARTICLE INFO

Keywords:
Common garden
Flower economics spectrum
Intraspecimen variability
Interspecific variability
Reproduction
Woody species

ABSTRACT

Floral traits represent a valuable yet underutilized resource for functional ecology. We aimed to examine the variability of six quantitative floral traits (carbon [C] and nitrogen [N] contents, C:N ratio, flower length and width, and dry biomass) among a randomly selected group of 79 temperate woody species at both interspecific and intraspecimen levels. We hypothesized that (1) flower traits are closely related to the evolutionary history of the species, resulting in a strong phylogenetic signal, and (2) flowers collected from the most and the least exposed to sunlight parts of the crown would not differ in trait values. We detected statistically significant phylogenetic signals for all six floral traits under study. We found significant differences between samples from the two light variants only for flower N content and C:N ratio. Given the substantial interspecific and the negligible intra-specimen variability observed, we are convinced that the incorporation of these studied traits, especially those related to flower size (i.e., dry biomass, length, and width), into research on flowering biology and ecology can significantly enrich our comprehension of the plant reproductive processes.

1. Introduction

Floral traits may represent a valuable yet underutilized resource in the field of functional ecology (Roddy et al., 2021). The current disregard for floral traits might appear confusing, as their inherent stability (Cresswell, 1998) could potentially simplify challenges associated with intraspecific variability and the extrapolation of trait values to other individuals of the same species (Albert et al., 2010, 2011; Cianciaruso et al., 2009). This stability could justify comparisons based on a smaller number of observations, given reduced intraspecific and intracanopy variability driven by environmental factors. Kleyer and Minden (2015) or Lefcheck et al. (2015) presented compelling arguments for considering functional traits from all plant organs to gain a comprehensive understanding of plant functionality. They emphasize that relying solely on data from a single organ, such as leaves, can lead to distorted results, particularly when viewed from an allocation-based perspective. Also, Pyšek et al. (2015) suggested that not all currently used traits are so relevant and that other traits might improve the accuracy of risk assessment in the case of invasion ecology. On the other hand, the variability of floral traits has also been detected for a number of different floral characteristics (Domínguez et al., 1998; Svensson, 1992).

Recognizing the profound implications of variability in functional traits of plants, numerous studies have been dedicated to examining the spatial and temporal distributions of their values (Dostál et al., 2020; Guang et al., 2019; Paź-Dyderska et al., 2020).

---

[*] Corresponding author.
E-mail address: sdyderska@man.poznan.pl (S. Paź-Dyderska).

https://doi.org/10.1016/j.gecco.2024.e03054
Received 8 January 2024; Received in revised form 19 May 2024; Accepted 19 June 2024

However, in the case of floral traits there is still a noticeable gap when it comes to their recognition. For instance, BIEN, one of the largest publicly available trait databases (accessed on 22.09.2023), includes information on maximum plant height for 3141 species, leaf area for 4128 species, and leaf nitrogen content for 3833 species (Maitner et al., 2018). It also offers data on various floral traits for a significant number of species, such as flower color (2623 species), flower pollination syndrome (2058 species), and plant flowering onset (4894 species) and duration (1659 species). However, quantitative floral traits receive considerably less attention, with only one floral trait included in the list (inflorescence length for 355 species), compared to 24 leaf-related traits. The TRY database includes over 550 leaf-related traits with more than 3.5 million measurements, but it covers only 124 traits and only 306,000 records related to flowers and inflorescences (Kattge et al., 2020).

The incorporation of floral traits into functional ecology remains relatively uncommon. This may be attributed to the challenges associated with collecting such data, such as the narrower time window for sampling in comparison to stems or leaves, or the absence of widely accepted protocols. However, over the past decade, there has been a notable increase in studies focusing on floral traits. One significant contribution to this field is the study "Towards the flower economics spectrum" by Roddy et al. (2021). In this study, the authors introduce the concept of the floral economics spectrum (FES), which examines various factors that can influence floral traits and functions. The primary hypothetical trade-offs within the FES framework include production costs, maintenance costs, and damage, which are represented by the relationship between flower mass per area (FMA) and flower longevity. The FES delineates four basic groups: (1) cheap, short-lived flowers (e.g., ruderals), (2) costly, short-lived flowers (e.g., cacti), (3) costly, long-lived flowers (e.g., orchids), and (4) cheap, long-lived flowers (currently unknown). Still, the authors suggest that empirical data should be used to validate the proposed occupied regions and their relationships between FMA and longevity. The FES concept is also supported by the study of E-Vojtkó et al. (2022), which demonstrates that floral and reproductive traits can be effectively integrated into the broader plant economics spectrum. Their findings indicate that floral traits are largely distinct from the leaf economics spectrum, providing novel insights into plant life strategies, although flower size scaled positively with leaf size. Overall, floral traits contribute to a unique aspect of variation in plant form and function, suggesting their distinct ecological significance within the plant economics spectrum. Furthermore, Lanuza et al. (2023) introduced the concept of the reproductive spectrum of flowering plants. Through analysis of a global dataset comprising 18 reproductive traits for 1506 species, they revealed that over 50 % of all trait variation is accounted for by the first two reproductive axes. These axes represent the negative correlation between flower number and flower size, as well as the negative correlation between autonomous selfing and floral display size. This study identified key reproductive trait correlations in flowering plants and elucidated their roles in shaping plant–pollinator interactions on a macro-ecological scale. The importance of integrating pollination-related traits has also been highlighted in the study of E-Vojtkó et al. (2020), as these often-overlooked floral characteristics can provide valuable insights into species coexistence patterns. To address current limitations, the authors suggest establishing standards for floral and pollination traits. They propose considering several groups of traits in future studies, such as flower color, display size, floral morphology, and floral reward production. However, as noted by the authors, a major obstacle to conducting more comprehensive analyses of floral traits at the community level is the lack of data, particularly in global trait databases.

The scarcity of data on floral traits also raises questions about uncertainties regarding their intraspecific (including intraspecimen) variability. Given the significant environmental variability observed in all functional traits at both inter- and intraspecific levels, a comprehensive understanding of the variability of floral traits becomes essential when attempting to successfully integrate them into the functional approach. Until now, most studies on the functional variability of floral traits across different species or within individual specimens have primarily concentrated on a limited number of taxa (González and Bello, 2009; Paglia et al., 2023; Żywiec et al., 2012). This limited exploration prompted us to investigate the range of variability in floral traits.

Our decision to initially focus exclusively on woody plants stems from the pioneering nature of our research in this area. We aimed to determine whether this research direction holds promise for future applications in both scientific and practical contexts. Concentrating on woody plants offers several advantages. Trees and shrubs play fundamental roles within ecosystems (Díaz et al., 2019; Ellison et al., 2005). They constitute a significant portion of ecosystem biomass and have the capacity to shape ecosystem functioning, influencing understory vegetation (Ampoorter et al., 2015; Barbier et al., 2008; Dyderski and Jagodziński, 2021), dependent animals and fungal assemblages (Jordano and Schupp, 2000; Łubek et al., 2019; Trocha et al., 2012), and nutrient cycling (Hobbie et al., 2006; Horodecki and Jagodziński, 2017; Mueller et al., 2012). Also, trees hold considerable economic importance, particularly in forest management, agriculture, or the wood industry (Seth, 2003). Therefore, we chose to focus solely on woody plants collected in a limited area under similar environmental conditions as the foundational framework for our study.

We aimed to examine the variability of six quantitative floral traits – carbon [C] content [%], nitrogen [N] content [%], C:N ratio [dimensionless], flower length [mm] and width [mm], and dry biomass [g] – among a randomly selected group of woody species growing under common garden conditions. We included flower C content in our analysis as carbon, acting as a structural component, can enhance durability and influence reward quality. N content is crucial for flower development and pollen production, impacting pollinator attraction and reward quality. Additionally, nitrogen-rich floral structures contribute to soil nutrient pools through post-pollination decomposition. The C:N ratio in flowers can provide insights into the allocation of carbon and nitrogen resources during flower development, affecting reproductive strategies and flower quality. Flower length and width play significant roles in attracting specific pollinators. Longer flowers may target pollinators with specific mouthparts, reflecting coevolutionary dynamics. Wider flowers accommodate bees, butterflies, and other pollinators seeking ample landing space, nectar, and pollen, thus influencing plant reproductive strategy. Lastly, flower dry biomass reflects the resources allocated to flower production, with higher dry biomass indicating greater reproductive investment by the plant. Larger, more attractive flowers with higher dry biomass tend to attract more pollinators, promoting successful pollination and seed set. On the other hand, smaller flowers may be less susceptible to damage by herbivores.

We hypothesized that (1) flower traits are closely related to the evolutionary history of the species, resulting in a strong phylogenetic signal. Natural selection tends to favor individuals with traits that are well-adapted to their environment and reproductive strategies. Thus, drastic changes to floral traits may be disadvantageous and selected against, leading to the conservatism of these traits within species over time. Thus, we anticipated a close connection of these traits to the species evolutionary history, and therefore phylogeny. Also, the convergence in floral traits is common in cases of plant species pollinated by functionally similar pollinator species (Anderson and Johnson, 2009; Bernhardt, 2000). This suggests that, due to lower environmental variability, it might be justifiable to extrapolate the values of these traits based on a smaller number of measurements compared to traits with higher variability (e.g., leaf traits). To explore the intraspecific variation in these traits, we compared samples from the same specimen but under different light conditions (Gratani et al., 2006; Paź-Dyderska et al., 2020; Rozendaal et al., 2006). Secondly, we hypothesized that (2) flowers collected from different parts of the crown would not exhibit significant differences in trait values. This assumption is grounded in the previously observed stability of reproduction-related traits. We assumed that factors such as light and heat exposure would not lead to significant diversification of flowers occurring in various parts of the crown.

2. Methods

2.1. Study area

When searching for opportunities to conduct comprehensive studies on functional traits, one often overlooked source of valuable data can be found within botanical gardens (Edwards et al., 2018; Fanal et al., 2021; Groover and Dosmann, 2012). These gardens meticulously curate collections of species from diverse regions, including areas with lower research activity compared to highly developed countries (Perez et al., 2019). Additionally, botanical gardens house a wide variety of species within relatively limited spaces, which greatly simplifies the collection of data. The similar conditions provided by botanical gardens facilitate comparisons of traits at both inter- and intraspecific levels, contributing to a more comprehensive understanding of trait variability.

We conducted our study within the Kórnik Arboretum (western Poland, 52.2448°N, 17.0969°E, 75 m a.s.l). This arboretum stands as one of Poland's oldest and most extensive collections, encompassing over 3500 taxa of woody plants, mostly ornamental cultivars. Observing plant traits, particularly in trees that require decades to mature, necessitates considering plant age. Consequently, the extensive dendrological collection within the Arboretum makes it an attractive setting for such research. We have already demonstrated the advantages of utilizing the Arboretum for conducting studies on specific leaf area (Paź-Dyderska et al., 2020), trade-offs between seed mass and resources (Dylewski et al., 2024), or the variability of floral chemical traits (Paź-Dyderska et al., 2022). The historical management of the Arboretum was focused on ornamental purposes, and therefore was not designed for ecological studies. While many specimens were densely planted, others stand isolated or in small groups, forming alleys. This can result in uneven light distribution among individuals. Nevertheless, the arboretum remains one of the best options for studying variability of traits across such a diverse array of species (Fanal et al., 2021; Groover and Dosmann, 2012; Paź-Dyderska et al., 2020).

The study site experiences a temperate climate with an average growing season lasting 220 days, mean annual precipitation of 544 mm, and a mean annual temperature of 8.3 °C. These climate parameters were recorded in the Arboretum between 1948 and 2005 (Cedro and Iszkuło, 2011). In 2021, when we collected the data, mean annual precipitation and mean annual temperatures were as follows: 527 mm and 10.5 °C, based on data from the nearest functioning meteorological station located in Poznań. The similar environmental conditions prevailing in the Arboretum, including the climate and soil type, warrant comparisons of traits across diverse systematic and functional groups. Consequently, the influence of climate variations and extreme conditions such as droughts, floods, or disturbances on the variability of traits studied was minimized. For that reason we assumed that the studied plants grow under conditions close to a common garden design.

2.2. Data collection

We selected a random sample of 79 woody plant species that were grown under common garden conditions (Paź-Dyderska et al., 2020) as an illustrative example. We aimed to assemble a phylogenetically balanced subset of taxa to ensure that our sample encompassed species from various families and representing different life strategies. Also, several practical considerations influenced our selection process. Some taxa were excluded as they were only ornamental cultivars, while others were either too juvenile or too mature to produce flowers. Additionally, changes in flowering phenology due to climate change posed challenges in tracking the blooming process and collecting fully developed flowers before wilting. Each species was represented by a single specimen since, despite the high number of taxa in the Arboretum, the majority of species are represented by singular individuals.

We collected data from March to July 2021, focusing on fully developed flowers without any damage, including signs of impact from fungi, herbivores, or abiotic factors like hail or drought. While not very widespread, there are existing collection protocols for floral traits. Therefore, we decided to incorporate some of the previous ideas that have been developed, as seen in studies conducted in botanical gardens (Roddy et al., 2016, 2019; Zhang et al., 2017). Additionally, we have already tested this protocol in our previous study on leaf and flower traits in the Arboretum (Paź-Dyderska et al., 2020, 2022). For example, during sample collection, we included both the pedicel and peduncle to ensure the durability of flowers, although those were not considered in size measurements or chemical analyses. We collected the flowers at the peak of the flowering process to ensure the full development of the floral organs while simultaneously ensuring that the flowers were in good condition. For dioecious species, our focus was exclusively on female flowers. This approach allowed us to match a singular value of each trait to each species, facilitating trait value comparisons across numerous species.

To assess the intra-canopy level of floral trait variability, we collected samples from two light variants of each specimen, specifically from the shadiest and sunniest sections of the crown, utilizing a 6 m long pole pruner. To reduce the influence of tree location on our findings, we gathered flowers exposed to sunlight from the southern sides of the crowns and flowers in shade from the northern sides. Most samples comprised ten flowers, resulting in a total of 20 flowers per specimen representing two light variants. However, exceptions occurred in cases where species produced exceptionally large flowers. For instance, with *Magnolia tripetala*, we chose to collect fewer flowers to avoid any harm to the valuable specimen. Similar to our previous study in the Arboretum, we selected flowers for the study based on qualitative observations, without measuring light availability (Paź-Dyderska et al., 2022). After collection, we placed the samples in ziplock bags not only to minimize the risk of damage to the fragile floral organs but also to prevent moisture loss, which could affect the size-related measurements. Subsequently, we stored them in a fridge to slow down wilting.

2.3. Traits measurements

We assessed the values of six traits for each sample: flower length [mm], width [mm], carbon content [%], nitrogen content [%], C:N ratio, and dry biomass [g, scale accuracy of 0.001]. In subsequent analyses, we used the mean values for each trait. We measured the length and width of individual flowers using electronic calipers [with an accuracy of 0.001 mm] within 24 hours of sample collection and calculated the mean values. Following this, all flowers were dried in an oven with forced air circulation at 65°C (ULE 600 and UF450, Memmert GmbH + Co. KG, Regensburg, Germany) until they reached a constant mass. We combined the flowers into pooled samples for analysis of C and N content, C:N ratio, and dry biomass. This resulted in two samples per specimen, representing two light variants. The pooled samples were analyzed directly to mitigate any bias stemming from the small sample sizes. We assessed the carbon content of samples using an ECS CHNS – O 4010 Elemental Combustion System (Costech Instruments, Italy/USA) and a CHNS/O Analyser 2400 Series II (Perkin Elmer, USA).

2.4. Data analysis

For data analysis we used R software (R Core Team, 2023). We assessed interspecific variability of traits in a quantified way using the coefficient of variation (CV). All mean values are followed by ± SE (standard error). To investigate whether interspecific variability in floral traits studied in woody species correlated with their phylogenesis, we acquired a phylogenetic tree from the V.PhyloMaker2 package (Jin and Qian, 2022). Subsequently, we examined Blomberg's K and Pagel's Λ phylogenetic correlation coefficients using the phylosignal package (Keck, 2023). To evaluate the impact of the light variant on the trait values, we conducted a phylogenetic paired

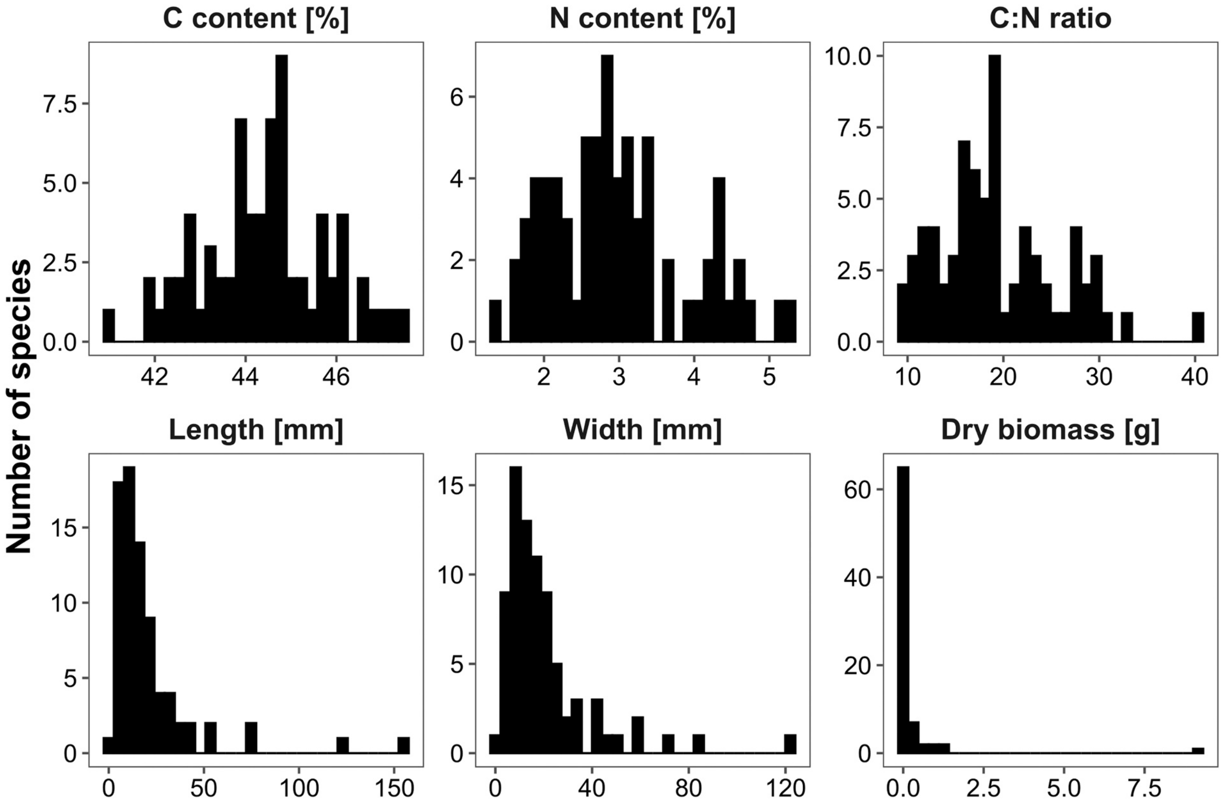


Fig. 1. Histograms visualizing distributions of the studied traits.

t-test using the phyl.pairedttest function from the phytools package (Revell, 2020). This test is an extension of the classical paired t-test linking observations due to their phylogenetic similarity. This allowed us to assess how canopy position might influence the variability of each species between samples representing the two light variants. We used the dplyr package for data processing, and ggplot2 for its visualization (Wickham et al., 2020a, 2020b).

3. Results

3.1. Ranges and distributions of studied traits

The carbon content in flowers of the studied species ranged from 40.91 % (*Euonymus atropurpureus*) to 47.41 % (*Viburnum sieboldii*), with an average of 44.42 % ± 0.16 (Fig. 1, Tables 1–2). This trait had the lowest CV among studied traits (3.09 %). Content of nitrogen in flowers ranged from 1.29 % (*Castanea sativa*) to 5.22 % (*Sambucus kamtschatica*), with an average of 2.97 % ± 0.1091 and a CV of 31.21 %. We found the lowest flower C:N ratio for *Calycanthus floridus* var. *glaucus* (9.81), while the highest for *C. sativa* (40.58), with an average of 19.43 % ± 0.74 and a CV of 32.41 %. For length and width, the lowest values were 0.68 mm and 0.61 mm (*Salix gracilistyla* in both cases), respectively, whereas the highest were 155.68 mm (*Davidia involucrata*) and 122.61 mm (*Magnolia tripetala*). The mean length was 20.65 ± 2.72 mm with the highest CV among the studied traits (117.19 %), while the mean width was 20.19 ± 2.21 mm, accompanied by a CV of 97.44 %. Single flower dry biomass ranged from 0.0001 g (*S. gracilistyla*) to 9.1655 g (*M. tripetala*), with an average of 0.2414 ± 0.1182 g and a CV of 435.14 %.

3.2. Relationships between traits and phylogenesis

We detected statistically significant phylogenetic signals for all six floral traits under study (Table 3, Figs. 2–3). According to both Blomberg's K and Pagel's Λ coefficients, the strongest evolutionary signal was found for dry biomass, followed by flower length. The weakest, but still statistically significant phylogenetic signal was observed in the C:N ratio, with C content following closely. In general, both chemical and morphological traits measured showed correlations with the evolutionary history of the species studied.

3.3. Differences between high-light and low-light flowers

We detected statistically significant differences between samples from the two light variants only in the case of flower N content and C:N ratio (Table 4, Fig. 4). The phylogenetic mean differences for those traits between the high-light and low-light variants were 0.1611 (95 % CI: 0.0390–0.2832) and −1.1832 (95 % CI: −2.1502 to −0.02136), respectively. The remaining traits did not show correlations between their intracanopy variability and the phylogenetic signal. In all cases, the trends between high-light and low-light parts of the crown have not been biologically significant. The minimum difference for C and N contents were 0.01 % (*Prunus padus* and *Cydonia oblonga*, respectively), 0.02 for C:N ratio (*Torminalis glaberrima*), 0.05 mm for length (*Hamamelis virginiana*), 0.02 mm for width (*Aesculus parviflora*), and <0.001 g for dry biomass (e.g., *Staphylea colchica*). The maximum difference for C content was 1.90 % (*Asimina triloba*), 2.26 % for N content (*Aesculus turbinata*), 18.27 for C:N ratio (*Paulownia tomentosa*), 58.45 mm for length (*Malus* ×*hartwigii*), 82.45 mm for width (*M.* ×*hartwigii*), and 5.42 g for dry biomass (*M.* ×*hartwigii*).

4. Discussion

In this study, we aimed to further enrich the dynamically developing field of functional ecology related to flowers. Thus, we introduced previously underappreciated floral traits and we adopted a multifaceted approach to assess their variability. We conducted an in-depth exploration of the variability and stability of novel floral traits. We focused on six traits that offered quantitative insights into the reproductive strategies of woody species: C and N content, the C:N ratio, floral length and width, and dry biomass. Through our analysis, we unveiled significant interspecific variability across these traits, showcasing a wide spectrum of diversity among the species under investigation. Additionally, we examined intraspecific differences influenced by light availability, revealing a low level of variation within the canopy of individual specimens. Furthermore, we investigated the correlation of these traits with the evolutionary history of the studied species, revealing statistically significant connections for all the traits under study.

Table 1
Descriptive statistics of studied traits. Abbreviations: N – number of sampled species, Min – minimum, Q1 – first quartile, SE – standard error, CV – coefficient of variation, Q3 – third quartile, Max – maximum. Due to small sample size it was impossible to obtain C and N content for five species.

Variable	N	Min	Q1	Median	Mean	SE	CV [%]	Q3	Max
C content [%]	72	40.91	43.63	44.58	44.42	0.16	3.09	45.25	47.41
N content [%]	72	1.30	2.27	2.85	2.97	0.11	31.21	3.37	5.22
C:N ratio	72	9.81	15.45	18.51	19.43	0.74	32.41	23.10	40.58
Length [mm]	79	0.68	8.20	14.03	20.66	2.72	117.19	21.05	155.68
Width [mm]	79	0.61	8.94	14.94	20.19	2.21	97.44	23.51	122.61
Dry biomass [g]	79	0.0001	0.0048	0.0365	0.2414	0.1182	435.14	0.1155	9.1655

Table 2
Overview of the species studied and their mean C content, N content, C:N ratio, length, width, and dry biomass values of the flowers.

Species	Family	C content [%]	N content [%]	C:N ratio	Length [mm]	Width [mm]	Dry biomass [g]
Acer pensylvanicum L.	Sapindaceae	44.170	4.650	11.077	12.241	8.260	0.026
Acer platanoides L.	Sapindaceae	44.005	3.865	13.288	7.378	10.839	0.047
Acer pseudoplatanus L.	Sapindaceae	44.400	3.155	16.406	9.575	9.187	0.037
Aesculus glabra Willd.	Sapindaceae	43.010	2.575	19.491	27.430	17.154	0.128
Aesculus hippocastanum L.	Sapindaceae	42.600	1.835	27.137	19.319	21.301	0.193
Aesculus parviflora Walter	Sapindaceae	41.920	2.680	18.696	51.255	20.945	0.088
Aesculus turbinata Blume	Sapindaceae	43.540	1.865	27.276	25.191	24.888	0.190
Ailanthus altissima (Mill.) Swingle	Simaroubaceae	44.645	3.450	15.190	7.917	8.561	0.019
Asimina triloba (L.) Dunal	Annonaceae	43.290	4.300	11.747	25.689	31.830	0.755
Berberis amurensis Rupr.	Berberidaceae	44.180	3.095	16.664	5.553	7.143	0.049
Berberis aquifolium Pursh	Berberidaceae	45.635	3.295	16.303	7.127	10.557	0.053
Berberis julianae C.K.Schneid	Berberidaceae	44.690	2.225	23.437	9.573	14.942	0.143
Calycanthus floridus var. *glaucus* (Willd.) Torr. & A.Gray	Calycanthaceae	43.340	5.185	9.809	38.765	33.974	0.875
Carpinus orientalis Mill.	Betulaceae	45.410	4.670	11.338	5.023	2.568	0.001
Castanea sativa Mill.	Fagaceae	44.865	1.295	40.576	8.479	9.814	0.018
Catalpa bignonioides Walter	Bignoniaceae	43.320	1.630	31.292	30.905	26.860	0.256
Cercidiphyllum japonicum Siebold & Zucc.	Cercidiphyllaceae	45.025	4.550	11.542	19.848	11.336	0.044
Cercis chinensis Bunge	Fabaceae	42.645	2.770	17.953	12.458	11.207	0.081
Chimonanthus praecox (L.) Link	Calycanthaceae	45.970	3.595	14.925	14.023	16.441	0.200
Chrysojasminum fruticans (L.) Banfi	Oleaceae	46.150	1.645	32.798	21.025	16.321	0.076
Cornus florida L.	Cornaceae	42.335	2.945	16.828	36.886	35.533	0.540
Cornus mas L.	Cornaceae	44.225	2.340	22.188	7.289	3.758	0.007
Cornus officinalis Siebold & Zucc.	Cornaceae	44.745	2.295	22.767	9.004	3.384	0.004
Corylopsis platypetala Rehder & E.H. Wilson	Hamamelidaceae	45.750	2.845	18.819	10.470	9.648	0.027
Corylopsis sinensis Hemsl.	Hamamelidaceae	44.830	2.810	18.626	10.802	8.694	0.038
Corylus avellana L.*	Betulaceae	-	-	-	4.113	3.016	0.004
Corylus ×colurnoides C.K.Schneid.*	Betulaceae	-	-	-	3.960	2.752	0.016
Crataegus holmesiana Ashe	Rosaceae	42.105	2.610	18.980	14.026	24.091	0.114
Crataegus submollis Sarg.	Rosaceae	43.820	2.905	17.643	10.510	17.016	0.091
Cydonia oblonga Mill.	Rosaceae	41.880	2.595	18.846	33.766	58.090	0.398
Daphne mezereum L.	Thymelaeaceae	43.660	3.120	16.307	10.507	11.150	0.039
Davidia involucrata Baill.	Nyssaceae	43.735	3.105	16.914	155.679	57.616	0.947
Euonymus atropurpureus Jacq.	Celastraceae	40.910	2.080	23.073	6.145	15.663	0.039
Exochorda racemosa (Lindl.) Rehder	Rosaceae	42.670	4.070	12.348	17.165	40.617	0.203
Forsythia giraldiana Lingelsh.	Oleaceae	44.610	2.650	19.646	29.746	29.071	0.129
Fothergilla latifolia J.F.Mill.	Hamamelidaceae	45.250	4.245	12.475	17.263	17.583	0.075
Fraxinus ornus L.	Oleaceae	46.010	2.780	19.452	9.180	7.847	0.002
Halesia carolina L.	Styracaceae	44.580	4.200	12.419	28.006	22.580	0.150
Hamamelis mollis Oliv.	Hamamelidaceae	46.130	2.120	26.023	14.849	22.925	0.096
Hamamelis virginiana L.	Hamamelidaceae	47.140	2.210	24.892	16.547	20.994	0.086
Ilex pedunculosa Miq.	Aquifoliaceae	46.025	2.845	18.978	5.980	10.651	0.083
Kolkwitzia amabilis Graebn.	Caprifoliaceae	43.880	1.765	28.991	19.071	19.823	0.080
Laburnum anagyroides Medik.	Fabaceae	43.185	4.375	11.513	19.507	15.824	0.117
Lonicera fragrantissima subsp. *fragrantissima*	Caprifoliaceae	44.085	3.295	15.586	17.266	14.436	0.051
Magnolia kobus DC.	Magnoliaceae	44.665	4.790	10.882	73.423	85.130	1.353
Magnolia stellata (Siebold & Zucc.) Maxim.	Magnoliaceae	44.300	4.385	11.831	54.990	71.272	1.280
Magnolia tripetala (L.) L.	Magnoliaceae	46.815	2.565	21.632	122.765	122.605	9.166
Malus baccata (L.) Moench	Rosaceae	43.865	2.135	23.939	22.517	43.704	0.128
Malus ×hartwigii Koehne	Rosaceae	44.670	2.535	20.987	17.107	40.602	0.027
Parrotia persica (DC.) C.A.Mey.	Hamamelidaceae	46.155	3.325	16.183	33.247	25.040	0.085
Paulownia tomentosa (Thunb.) Steud.	Paulowniaceae	44.735	1.840	28.358	75.027	50.245	0.254
Prunus incisa Thunb.	Rosaceae	42.830	3.650	13.755	11.957	25.753	0.007
Prunus laurocerasus L.	Rosaceae	45.605	2.115	25.111	15.047	16.031	0.012
Prunus padus L.	Rosaceae	44.655	2.655	19.609	6.337	12.993	0.003
Prunus serrulata Lindl.	Rosaceae	42.770	2.905	17.292	18.864	29.089	0.009
Quercus rubra L.*	Fagaceae	-	-	-	4.075	3.525	0.001
Rhododendron luteum Sweet	Ericaceae	44.780	2.910	17.956	42.730	46.107	0.033
Rhus aromatica Aiton	Anacardiaceae	47.075	3.190	17.220	3.466	3.435	0.001
Salix gracilistyla Miq.*	Salicaceae	-	-	-	0.681	0.609	0.000
Sambucus kamtschatica E.Wolf	Adoxaceae	44.710	5.220	9.995	4.344	5.187	0.001
Sorbaria kirilowii (Regel) Maxim.	Rosaceae	44.745	2.685	19.450	7.195	9.537	0.004
Sorbus aucuparia L.	Rosaceae	44.315	2.280	22.698	8.332	10.861	0.004
Spiraea longigemmis Maxim.	Rosaceae	44.585	3.345	15.542	7.560	7.999	0.001

(*continued on next page*)

Table 2 (*continued*)

Species	Family	C content [%]	N content [%]	C:N ratio	Length [mm]	Width [mm]	Dry biomass [g]
Spiraea media F.Schmidt	Rosaceae	44.900	3.080	17.216	6.526	9.249	0.002
Spiraea ×nudiflora Zabel	Rosaceae	45.380	2.995	17.877	10.914	19.164	0.004
Staphylea colchica Stev.	Staphyleaceae	42.860	4.530	11.063	10.462	7.350	0.007
Staphylea pinnata L.	Staphyleaceae	42.385	4.330	12.234	20.536	14.473	0.009
Syringa josikaea J.Jacq. ex Rchb.	Oleaceae	46.630	2.000	27.257	14.796	7.643	0.002
Syringa pubescens subsp. *pubescens*	Oleaceae	45.730	1.770	30.141	15.214	7.310	0.003
Syringa vulgaris L.	Oleaceae	44.385	3.445	15.086	21.072	20.377	0.009
Tilia americana L.	Malvaceae	43.830	1.705	29.972	14.564	17.707	0.012
Torminalis glaberrima (Gand.) Sennikov & Kurtto	Rosaceae	43.845	2.090	24.456	8.448	11.285	0.006
Viburnum carlesii Hemsl. ex Forbes & Hemsl.	Adoxaceae	46.490	2.775	23.196	16.333	12.059	0.006
Viburnum farreri Stearn*	Adoxaceae	-	-	-	10.087	7.914	0.002
Viburnum lantana L.	Adoxaceae	47.245	2.430	22.774	12.718	9.798	0.003
Viburnum sieboldii Miq.	Adoxaceae	47.405	3.030	18.399	8.060	11.366	0.004
Weigela florida (Bunge) A.DC.	Caprifoliaceae	43.900	1.890	27.495	44.448	22.784	0.022
Zabelia tyaihyoni (Nakai) Hisauti & H. Hara	Caprifoliaceae	45.265	1.965	29.263	16.652	16.716	0.006
Zelkova serrata (Thunb.) Makino	Ulmaceae	44.955	3.330	15.766	4.775	3.510	0.002

* Due to small sample size it was impossible to obtain C and N content for five species.

Table 3
Strength of phylogenetic signals in traits assessed using Blomberg's K and Pagel's Λ and p-values of these coefficients assessed using the phyloSignal() function from the phylosignal package (Keck, 2023).

Variable	Blomberg's K	p-value	Pagel's Λ	p-value
C content [%]	0.335	<0.001	0.700	<0.001
N content [%]	0.402	<0.001	0.822	<0.001
C:N ratio	0.312	0.002	0.675	0.014
Length [mm]	0.827	<0.001	1.006	<0.001
Width [mm]	0.748	<0.001	0.945	<0.001
Dry biomass [g]	0.864	0.012	1.012	<0.001

4.1. *Interspecific variability of the floral traits studied*

We observed interspecific variability among the studied species, with the highest variability in size-related traits (dry biomass, length, and width), and the lowest variability in chemical traits (C and N content, and C:N ratio). Specifically, we noticed that among the traits examined, dry biomass exhibited the highest interspecific variability, while C content showed the lowest. In general, significant interspecific variability within a functional trait is valuable when exploring potential differences among species and their flowering strategies. A high biomass indicates a larger investment in individual flowers, enhancing their durability and attractiveness. Conversely, a small flower biomass suggests the dispersal of reproductive risks over a large number of flowers. This trade-off is in line with the findings of Lanuza et al. (2023), who proved the negative correlation between flower number and flower size. In the context of our study, this trade-off is particularly evident in the case of size-related traits, as opposed to chemical traits. This is in line with our previous findings from a study on interspecific variability of herbaceous species' traits, where we found that 37 % of the variability in performance-related traits, such as biomass, was attributed to species identity, while 38 % was linked to the collection site. For Specific Leaf Area (SLA), a structure-related trait, we demonstrated that 58 % of the variability was associated with species identity, and 24 % was influenced by the collection site. It's worth noting that even traits with a strong species-specific component, such as SLA, can exhibit significant variation throughout the growing season, contributing to increased intraspecific variability. However, for flowers, which must be collected within a relatively narrow time window from emergence, this variability naturally tends to decrease. For example, in his comprehensive literature review, Cresswell (1998) highlighted that traits associated with the mechanical fit between flowers and pollinators, i.e. those related to size, exhibited the least variability. Thus, maintaining low variability in these traits may reflect a strategy related to animal pollination, while for wind- or water-pollinated plants, variability may be more common. However, it remains challenging to find comparative data for numerous floral traits across numerous species, as this branch of functional ecology is still advancing.

We found a statistically significant phylogenetic signal for all the traits we studied, indicating a strong correlation between floral traits and the evolutionary history of species. Our study included plant materials from a diverse set of 79 species, a sample size robust enough for phylogenetic analysis. Previous studies have highlighted correlations between functional traits and the evolutionary history of species, such as the root-to-shoot ratio (Burns and Strauss, 2012), SLA (Paź-Dyderska et al., 2020), seed mass variation (Zhang et al., 2020), or wood carbon concentration (Martin et al., 2018). However, when it comes to floral traits, such studies have been relatively scarce. In our previous investigations of chemical floral traits, we did not observe phylogenetic signals in the values of

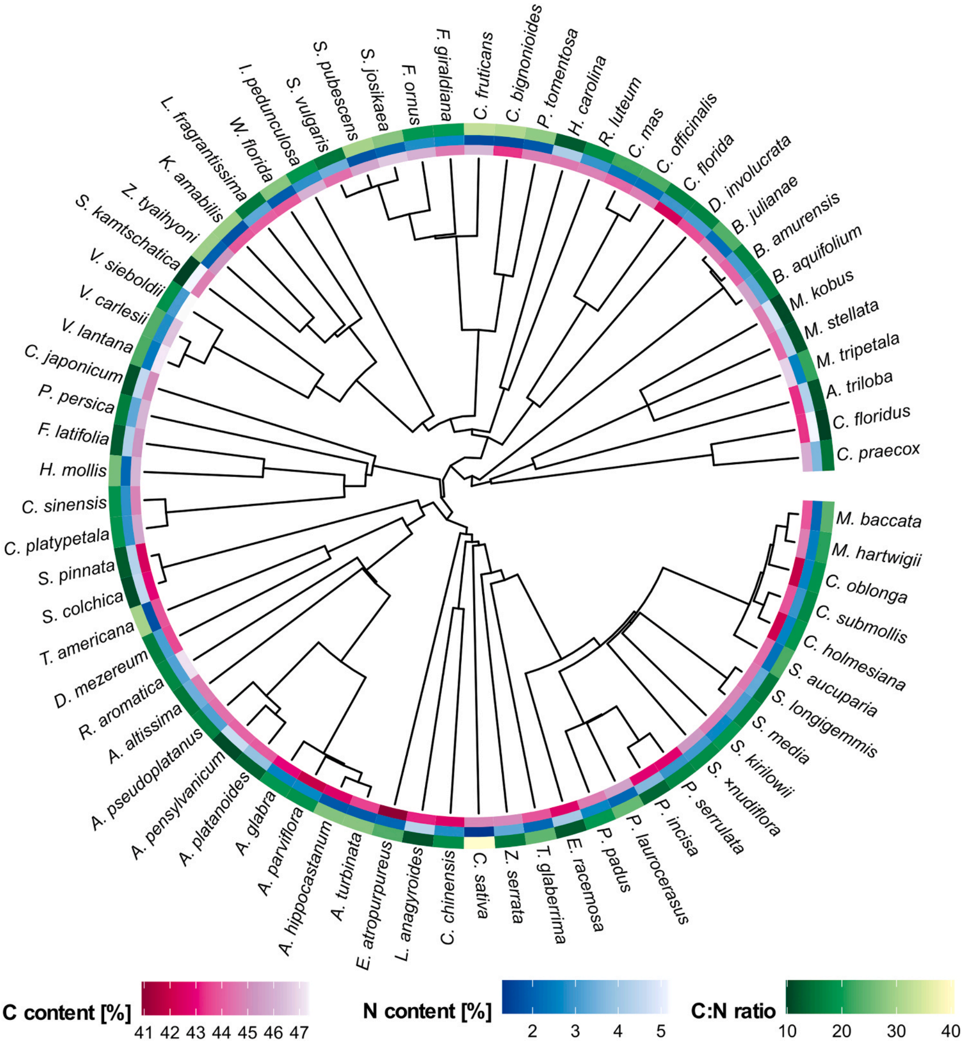


Fig. 2. Distributions of chemical traits across the phylogenetic trees.

soluble carbohydrates and total non-structural carbohydrates, while we found such a signal in starch and phenolic compound contents (Paź-Dyderska et al., 2022). There we suggested that phylogenetically clustered plants might exhibit higher functional variability, which could be interpreted as a mechanism for stabilizing the coexistence of a group of evolutionarily related species (Castro et al., 2018).

This discrepancy might be attributed to the choice of traits. Previously analyzed chemical traits, including certain carbohydrate and phenolic compounds, are closely tied to pollination processes, which can vary even among closely related species (Stone et al., 1998). This variability can function as a natural barrier preventing cross-fertilization among closely related species. On the other hand, in this study, traits such as C and N content are noted for their stability across various plant organs. Additionally, size-related traits, such as similar length and width, can be indicators of species relatedness, without necessarily increasing the risk of cross-fertilization of closely related species. This risk can significantly affect population viability, thus leading to the decline of inbreeding individuals (Bulman et al., 2007; Stone et al., 1998). The notable correlation observed between the studied traits and the evolutionary history of species can be attributed to the convergence of floral characteristics in species closely linked to specific pollinators (Anderson and Johnson, 2009; Armbruster et al., 2000; Bernhardt, 2000). This convergence suggests a dynamic relationship where certain species develop similar floral traits to optimize interactions with particular pollinators. However, as we stated above, closely related and competing species may diverge in their floral traits as a strategic mechanism to diminish the risk of cross-breeding. This divergence serves as an adaptive response, ensuring reproductive isolation between these closely related species (Stone et al., 1998).

4.2. Intraspecimen variability of the floral traits studied

In terms of intra-specimen variability, we confirmed a negligible level of differences in trait values collected from different light

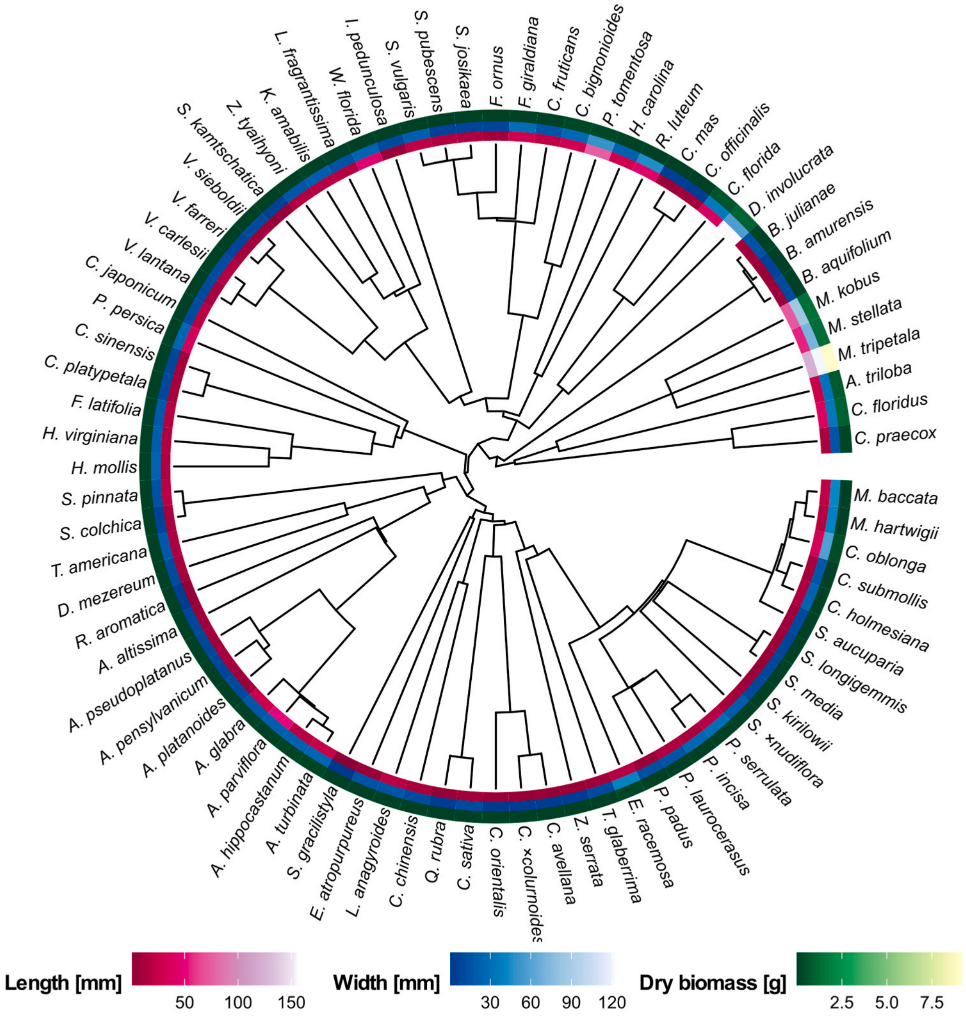


Fig. 3. Distributions of morphological traits across the phylogenetic trees.

Table 4

Parameters of phylogenetic paired t-tests of flower traits. Abbreviations: 95 %CI – 95 % confidence intervals, t – test statistic, df – degrees of freedom.

Variable	Phylogenetic mean difference	95 %CI lower	95 %CI upper	t	df	p-value	log-likelihood
C content [%]	0.0714	-0.0998	0.2426	0.8177	69	0.4164	-80.5802
N content [%]	0.1611	0.0390	0.2832	2.5866	69	**0.0118**	-56.2469
C:N ratio	-1.1832	-2.1502	-0.2163	-2.3984	69	**0.0192**	-198.9920
Length [mm]	3.0650	-4.1430	10.2730	0.8334	76	0.4072	-275.4450
Width [mm]	-2.0681	-12.4958	8.3596	-0.3887	76	0.6986	-294.0230
Dry biomass [g]	0.1766	-0.3388	0.6921	0.6716	76	0.5039	-56.4569

availability conditions within the same specimen. Samples from high-light and low-light conditions, representing opposing light and heat exposures, did not exhibit statistically significant differences, thus we did not reject hypothesis 2. Several reasons might explain this observation. In the context of zoophilous flowers, plant-pollinator interactions play a crucial role, particularly in inducing stabilizing selection on floral structures (Cresswell, 1998). This selection mechanism promotes the recurrence of specific floral traits, ensuring a consistent compatibility between insect structures and the flowers they pollinate. Maintaining this stability is vital, as excessive variability in floral structures could potentially hinder the effectiveness of pollination, limiting the plant's ability to pollinate a maximum number of flowers. However, it is important to note that pollinator-mediated selection, while significant, does not provide a full explanation for the variation in floral traits (Galen, 1999). The morphological features of each plant are subject to a myriad of diverse and sometimes conflicting selection pressures (Galen, 1999), suggesting that the interplay of various factors contributes to the intricate diversity observed in floral characteristics. For example, in the case of wild radish, Williams and Conner (2001) found, contrary to their expectations, a higher level of within-specimen variation compared to among-plant variation, similar to Campbell's

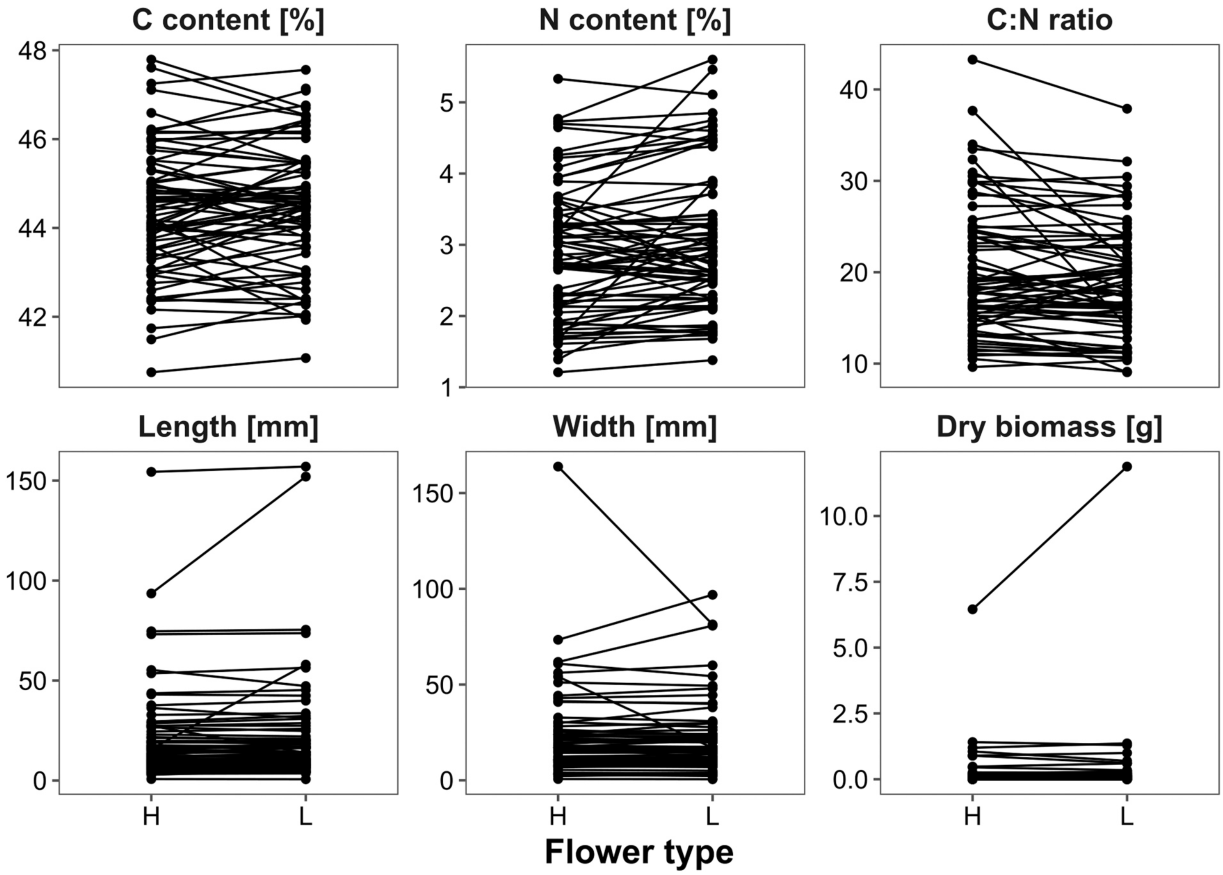


Fig. 4. Comparison of flower traits between high-light and low-light. Lines represent slope of trait differences for a particular species. Results of formal tests – Table 4.

(1989) observations. This could imply that greater phenotypic variation within individuals, as opposed to among individuals, might weaken selection pressure and evolutionary outcomes.

Secondly, the low intra-specimen variability in floral traits may be attributed to the fact that a significant portion of woody species adopt a strategy of producing flowers before the development of leaves. In the case of trees and shrubs, leaves are the primary factor limiting light and heat availability. As a result, in the absence of leaves, variations in light and heat conditions among different parts of the specimen remain inconspicuous. This prevents significant intra-specimen variations, as seen, for example, in the case of specific leaf area, which can vary by over 40 % within leaves collected from the same specimen (Paź-Dyderska et al., 2020). That way species representing this strategy would benefit from relatively constant environmental conditions within the canopy, stabilizing the morphology and chemical composition of flowers. Thirdly, some of the studied species reach relatively low heights, potentially physically limiting the variation in light and heat conditions among different parts of the specimen.

4.3. *Study limitations*

We encountered certain trade-offs during the planning phase of our study, contributing to some of its limitations. As we have already stated, we focused exclusively on woody plants, based on a number of arguments presented in the Introduction section. On the other hand, collecting samples from herbaceous species using our proposed methodological approach would prove considerably more challenging, requiring the acquisition of a diverse array of herbaceous species for common garden conditions. Therefore, we have chosen to utilize our extensive historical dendrological collection at Kórnik Arboretum, concentrating our research efforts on woody plant species.

We chose to include just one representative specimen per species to encompass a greater diversity of species in our study. While there hasn't been a definitive determination of the ideal sample size for studying the intraspecific variability of flowers, previous research on foliar traits suggests that the most accurate sampling size includes four samples from ten individuals (Petruzzellis et al., 2017). Although we recognize that a larger number of specimens would provide a more comprehensive representation of data variability, we opted to collect flowers from individual specimens. This decision was influenced not only by the layout of the Arboretum, which frequently features only one mature specimen of each species, but also by the labor-intensive nature of data collection. Given that the flowering periods of various species often overlap and fluctuate from year to year, collecting flowers required continuous monitoring of flower development stages for all species throughout the growing season, as well as waiting for the optimal flowering phase to gather material for each species. Consequently, the process of collecting flowers is more time-consuming compared to, for instance, collecting leaves. Nevertheless, such data holds significant potential for future applications in the field of functional ecology. We also believe that, akin to our previous studies (Paź-Dyderska et al., 2020, 2022), employing a common garden design for our research (in which numerous species grow in a single area with similar climatic conditions) mitigates some of the challenges posed by the aforementioned limitations.

The nature of flowering, which occurs at various times throughout the growing season, made it impractical to collect data at a single time point, unlike leaves that remain available for months during the vegetative season. Additionally, we recognize that flowers, much like other plant organs, exhibit seasonal variations in their chemical composition, encompassing both the C and N content analyzed in our study and other constituents (Ernst et al., 1991; Kenis et al., 1985; McMann et al., 2022). Nevertheless, our investigation is among the pioneering efforts to explore the potential of C and N content in flowers for applications in the field of functional ecology. Consequently, we made a conscious decision to temporarily overlook this type of variability, considering it of minimal significance at this stage of the field's development.

5. Conclusions

Our findings constitute a substantial contribution to the field of flower production-related strategies among woody plants. We present data on six quantitative floral traits of 79 temperate woody species. We identified a statistically significant correlation between all the proposed traits and their evolutionary history. We have uncovered a limited influence of light availability on the intra-specimen variation of the floral traits studied, with statistically significant intra-specimen differences occurring only for flower N content and C:N ratio. This finding underscores the potential of these traits for functional ecology. Given the substantial interspecific variation and the negligible intra-specimen variability observed in the traits we have examined, we are convinced that the incorporation of these studied traits, especially those related to flower size (dry biomass, length, and width), into research on flowering biology and ecology can significantly enrich our comprehension of the crucial reproductive processes.

Funding

This work was supported by the National Science Centre, Poland [grant number 2020/37/N/NZ8/00387], and partially supported by the Institute of Dendrology of the Polish Academy of Sciences.

CRediT authorship contribution statement

Conceptualization, S.P.-D. and A.M.J.; methodology, S.P.-D. and A.M.J.; software, S.P.-D.; validation, S.P.-D.; formal analysis, S.P.-D.; investigation, S.P.-D.; data curation, S.P.-D.; writing—original draft preparation, S.P.-D.; writing—review and editing, A.M.J.; visualization, S.P.-D.; supervision, A.M.J.; project administration, S.P.-D.; and funding acquisition, S.P.-D. and A.M.J. Both authors have read and agreed to the published version of the manuscript.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Acknowledgments

We would like to thank Kinga Nowak for her invaluable assistance in the selection of species that align with the goals of our research. We express our appreciation to Marcin K. Dyderski for his insightful and constructive feedback on the manuscript.

Declaration of Generative AI and AI-assisted technologies in the writing process

During the preparation of this work the authors used ChatGPT in order to enhance the grammar and clarity of the manuscript. After using this tool, the authors reviewed and edited the content as needed and take full responsibility for the content of the publication.

References

Albert, C.H., Grassein, F., Schurr, F.M., Vieilledent, G., Violle, C., 2011. When and how should intraspecific variability be considered in trait-based plant ecology? Perspect. Plant Ecol. Evol. Syst. 13, 217–225. https://doi.org/10.1016/j.ppees.2011.04.003.

Albert, C.H., Thuiller, W., Yoccoz, N.G., Soudant, A., Boucher, F., Saccone, P., Lavorel, S., 2010. Intraspecific functional variability: extent, structure and sources of variation. J. Ecol. 98, 604–613. https://doi.org/10.1111/j.1365-2745.2010.01651.x.

Ampoorter, E., Baeten, L., Vanhellemont, M., Bruelheide, H., Scherer-Lorenzen, M., Baasch, A., Erfmeier, A., Hock, M., Verheyen, K., 2015. Disentangling tree species identity and richness effects on the herb layer: first results from a German tree diversity experiment. J. Veg. Sci. 26, 742–755. https://doi.org/10.1111/jvs.12281.

Anderson, B., Johnson, S.D., 2009. Geographical covariation and local convergence of flower depth in a guild of fly-pollinated plants. New Phytol. 182, 533–540. https://doi.org/10.1111/j.1469-8137.2009.02764.x.

Armbruster, S., Fenster, C., Dudash, M., 2000. Pollination "principles" revisited: specialization, pollination syndromes, and the evolution of flowers. Scand. Assoc. Pollinat. Ecol. Honours Knut Faegri 39, 179–200.

Barbier, S., Gosselin, F., Balandier, P., 2008. Influence of tree species on understory vegetation diversity and mechanisms involved—a critical review for temperate and boreal forests. For. Ecol. Manag. 254, 1–15. https://doi.org/10.1016/j.foreco.2007.09.038.

Bernhardt, P., 2000. Convergent evolution and adaptive radiation of beetle-pollinated angiosperms. In: Dafni, A., Hesse, M., Pacini, E. (Eds.), Pollen and Pollination. Springer, Vienna, pp. 293–320. https://doi.org/10.1007/978-3-7091-6306-1_16.

Bulman, C.R., Wilson, R.J., Holt, A.R., Bravo, L.G., Early, R.I., Warren, M.S., Thomas, C.D., 2007. Minimum viable metapopulation size, extinction debt, and the conservation of a declining species. Ecol. Appl. 17, 1460–1473. https://doi.org/10.1890/06-1032.1.

Burns, J.H., Strauss, S.Y., 2012. Effects of competition on phylogenetic signal and phenotypic plasticity in plant functional traits. Ecology 93, S126–S137. https://doi.org/10.1890/11-0401.1.

Campbell, D.R., 1989. Measurements of selection in a hermaphroditic plant: variation in male and female pollination success. Evolution 43, 318–334. https://doi.org/10.1111/j.1558-5646.1989.tb04230.x.

Castro, S.A.B., Silveira, F.A.O., Marcato, M.S., Lemos-Filho, J.P., 2018. So close, yet so different: Divergences in resource use may help stabilize coexistence of phylogenetically-related species in a megadiverse grassland. Flora, Plant life Campo Rupestre, a Megadiverse Neotrop. Old. -Growth Grassl. 238, 72–78. https://doi.org/10.1016/j.flora.2016.11.018.

Cedro, A., Iszkuło, G., 2011. Do females differ from males of European Yew (*Taxus baccata* L.) in Dendrochronological analysis? Tree Ring Res. 67, 3–11. https://doi.org/10.3959/2009-9.1.

Cianciaruso, M.V., Batalha, M.A., Gaston, K.J., Petchey, O.L., 2009. Including intraspecific variability in functional diversity. Ecology 90, 81–89. https://doi.org/10.1890/07-1864.1.

Cresswell, J.E., 1998. Stabilizing Selection and the Structural Variability of Flowers within Species. Ann. Bot. 81, 463–473. https://doi.org/10.1006/anbo.1998.0594.

Díaz, S., Settele, J., Brondízio, E., Ngo, H., Guèze, M., Agard, J., Arneth, A., Balvanera, P., Brauman, K., Butchart, S., Chan, K., Garibaldi, L., Ichii, K., Liu, J., Subrmanian, S., Midgley, G., Miloslavich, P., Molnár, Z., Obura, D., Pfaff, A., Polasky, S., Purvis, A., Razzaque, J., Reyers, B., Chowdhury, R., Shin, Y., Visseren-Hamakers, I., Wilis, K., Zayas, C., 2019. Summary for policymakers of the global assessment report on biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem. https://files.ipbes.net/ipbes-web-prod-public-files/downloads/spm_unedited_advance_for_posting_htn.pdf.

Domínguez, C.A., Eguiarte, L.E., Núñez-Farfán, J., Dirzo, R., 1998. Flower morphometry of *Rhizophora mangle* (Rhizophoraceae): geographical variation in Mexican populations. Am. J. Bot. 85, 637–643. https://doi.org/10.2307/2446532.

Dostál, P., Fischer, M., Prati, D., 2020. Comparing experimental and field-measured traits and their variability in Central European grassland species. J. Veg. Sci. 31, 561–570. https://doi.org/10.1111/jvs.12875.

Dyderski, M.K., Jagodziński, A.M., 2021. Impacts of invasive trees on alpha and beta diversity of temperate forest understories. Biol. Invasions 23, 235–252. https://doi.org/10.1007/s10530-020-02367-6.

Dylewski, Ł., Adamczyk, D., Żytkowiak, R., Jagodziński, A.M., 2024. Seed mass and seed resources – testing the defense trade-off hypothesis in woody plants. Dendrobiology 91, 32–41. https://doi.org/10.12657/denbio.091.003.

Edwards, C.E., Bassüner, B., Birkinshaw, C., Camara, C., Lehavana, A., Lowry, P.P., Miller, J.S., Wyatt, A., Jackson, P.W., 2018. A botanical mystery solved by phylogenetic analysis of botanical garden collections: the rediscovery of the presumed-extinct *Dracaena umbraculifera*. Oryx 52, 427–436. https://doi.org/10.1017/S0030605317001570.

Ellison, A.M., Bank, M.S., Clinton, B.D., Colburn, E.A., Elliott, K., Ford, C.R., Foster, D.R., Kloeppel, B.D., Knoepp, J.D., Lovett, G.M., Mohan, J., Orwig, D.A., Rodenhouse, N.L., Sobczak, W.V., Stinson, K.A., Stone, J.K., Swan, C.M., Thompson, J., Holle, B.V., Webster, J.R., 2005. Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. Front. Ecol. Environ. 3, 479–486. https://doi.org/10.1890/1540-9295(2005)003[0479:LOFSCF]2.0.CO;2.

Ernst, W.H.O., Kuiters, A.T., Nelissen, H.J.M., Tolsma, D.J., 1991. Seasonal variation in phenolics in several savanna tree species in Botswana. Acta Bot. Neerl. 40, 63–74. https://doi.org/10.1111/j.1438-8677.1991.tb01514.x.

E-Vojtkó, A., de Bello, F., Durka, W., Kühn, I., Götzenberger, L., 2020. The neglected importance of floral traits in trait-based plant community assembly. J. Veg. Sci. 31, 529–539. https://doi.org/10.1111/jvs.12877.

E-Vojtkó, A., Junker, R.R., de Bello, F., Götzenberger, L., 2022. Floral and reproductive traits are an independent dimension within the plant economic spectrum of temperate central Europe. New Phytol. 236, 1964–1975. https://doi.org/10.1111/nph.18386.

Fanal, A., Mahy, G., Fayolle, A., Monty, A., 2021. Arboreta reveal the invasive potential of several conifer species in the temperate forests of western Europe. NeoBiota 64, 23–42. https://doi.org/10.3897/neobiota.64.56027.

Galen, C., 1999. Why Do Flowers Vary? The functional ecology of variation in flower size and form within natural plant population. BioScience 49, 631–640. https://doi.org/10.2307/1313439.

González, F., Bello, M.A., 2009. Intra-individual variation of flowers in *Gunnera* subgenus Panke (Gunneraceae) and proposed apomorphies for Gunnerales. Bot. J. Linn. Soc. 160, 262–283. https://doi.org/10.1111/j.1095-8339.2009.00974.x.

Gratani, L., Covone, F., Larcher, W., 2006. Leaf plasticity in response to light of three evergreen species of the Mediterranean maquis. Trees 20, 549–558. https://doi.org/10.1007/s00468-006-0070-6.

Groover, A., Dosmann, M., 2012. The importance of living botanical collections for plant biology and the "next generation" of evo-devo research. Front. Plant Sci. 3 https://doi.org/10.3389/fpls.2012.00137.

Guang, Z., Xu, Z., Du, W., Yu, J., Meng, S., Liu, Q., 2019. Seasonal variability of functional traits of understory herbs in a broad-leaved Korean pine forest. Russ. J. Ecol. 50, 583–586. https://doi.org/10.1134/S1067413619060146.

Hobbie, S.E., Reich, P.B., Oleksyn, J., Ogdahl, M., Zytkowiak, R., Hale, C., Karolewski, P., 2006. Tree species effects on decomposition and forest floor dynamics in a common garden. Ecology 87, 2288–2297. https://doi.org/10.1890/0012-9658(2006)87[2288:TSEODA]2.0.CO;2.

Horodecki, P., Jagodziński, A.M., 2017. Tree species effects on litter decomposition in pure stands on afforested post-mining sites. For. Ecol. Manag. 406, 1–11. https://doi.org/10.1016/j.foreco.2017.09.059.

Jin, Y., Qian, H., 2022. V.PhyloMaker2: An updated and enlarged R package that can generate very large phylogenies for vascular plants. Plant Divers. 44, 335–339. https://doi.org/10.1016/j.pld.2022.05.005.

Jordano, P., Schupp, E.W., 2000. Seed disperser effectiveness: the quantity component and patterns of seed rain for *Prunus mahaleb*. Ecol. Monogr. 70, 591–615. https://doi.org/10.1890/0012-9615(2000)070[0591:SDETQC]2.0.CO;2.

Kattge, J., Bönisch, G., Díaz, S., Lavorel, S., Prentice, I.C., Leadley, P., Tautenhahn, S., Werner, G.D.A., Aakala, T., Abedi, M., Acosta, A.T.R., Adamidis, G.C., Adamson, K., Aiba, M., Albert, C.H., Alcántara, J.M., C, C.A, Aleixo, I., Ali, H., Amiaud, B., Ammer, C., Amoroso, M.M., Anand, M., Anderson, C., Anten, N., Antos, J., Apgaua, D.M.G., Ashman, T.-L., Asmara, D.H., Asner, G.P., Aspinwall, M., Atkin, O., Aubin, I., Baastrup-Spohr, L., Bahalkeh, K., Bahn, M., Baker, T., Baker, W.J., Bakker, J.P., Baldocchi, D., Baltzer, J., Banerjee, A., Baranger, A., Barlow, J., Barneche, D.R., Baruch, Z., Bastianelli, D., Battles, J., Bauerle, W., Bauters, M., Bazzato, E., Beckmann, M., Beeckman, H., Beierkuhnlein, C., Bekker, R., Belfry, G., Belluau, M., Beloiu, M., Benavides, R., Benomar, L., Berdugo-Lattke, M.L., Berenguer, E., Bergamin, R., Bergmann, J., Carlucci, M.B., Berner, L., Bernhardt-Römermann, M., Bigler, C., Bjorkman, A.D., Blackman, C., Blanco, C., Blonder, B., Blumenthal, D., Bocanegra-González, K.T., Boeckx, P., Bohlman, S., Böhning-Gaese, K., Boisvert-Marsh, L., Bond, W., Bond-Lamberty, B., Boom, A., Boonman, C.C.F., Bordin, K., Boughton, E.H., Boukili, V., Bowman, D.M.J.S., Bravo, S., Brendel, M.R., Broadley, M.R., Brown, K.A., Bruelheide, H., Brumnich, F., Bruun, H.H., Bruy, D., Buchanan, S.W., Bucher, S.F., Buchmann, N., Buitenwerf, R., Bunker, D.E., Bürger, J., Burrascano, S., Burslem, D.F.R.P., Butterfield, B.J., Byun, C., Marques, M., Scalon, M.C., Caccianiga, M., Cadotte, M., Cailleret, M., Camac, J., Camarero, J.J., Campany, C., Campetella, G., Campos, J.A., Cano-Arboleda, L., Canullo, R., Carbognani, M., Carvalho, F., Casanoves, F., Castagneyrol, B., Catford, J.A., Cavender-Bares, J., Cerabolini, B.E.L., Cervellini, M., Chacón-Madrigal, E., Chapin, K., Chapin, F.S., Chelli, S., Chen, S.-C., Chen, A., Cherubini, P., Chianucci, F., Choat, B., Chung, K.-S., Chytrý, M., Ciccarelli, D., Coll, L., Collins, C.G., Conti, L., Coomes, D., Cornelissen, J.H.C., Cornwell, W.K., Corona, P., Coyea, M., Craine, J., Craven, D., Cromsigt, J.P.G.M., Csecserits, A., Cufar, K., Cuntz, M., Silva, A.C. da, Dahlin, K.M., Dainese, M., Dalke, I., Fratte, M.D., Dang-Le, A.T., Danihelka, J., Dannoura, M., Dawson, S., Beer, A.J. de, Frutos, A.D., Long, J.R.D., Dechant, B., Delagrange, S., Delpierre, N., Derroire, G., Dias, A.S., Diaz-Toribio, M.H., Dimitrakopoulos, P.G., Dobrowolski, M., Doktor, D., Dřevojan, P., Dong, N., Dransfield, J., Dressler, S., Duarte, L., Ducouret, E., Dullinger, S., Durka, W., Duursma, R., Dymova, O., E-Vojtkó, A., Eckstein, R.L., Ejtehadi, H., Elser, J., Emilio, T., Engemann, K., Erfanian, M.B., Erfmeier, A., Esquivel-Muelbert, A., Esser, G., Estiarte, M., Domingues, T.F., Fagan, W.F., Fagúndez, J., Falster, D.S., Fan, Y., Fang, J., Farris, E., Fazlioglu, F., Feng, Y., Fernandez-Mendez, F., Ferrara, C., Ferreira, J., Fidelis, A., Finegan, B., Firn, J., Flowers, T.J., Flynn, D.F.B., Fontana, V., Forey, E., Forgiarini, C., François, L., Frangipani, M., Frank, D., Frenette-Dussault, C., Freschet, G.T., Fry, E.L., Fyllas, N.M., Mazzochini, G.G., Gachet, S., Gallagher, R., Ganade, G., Ganga, F., García-Palacios, P., Gargaglione, V., Garnier, E., Garrido, J.L., Gasper, A.L. de, Gea-Izquierdo, G., Gibson, D., Gillison, A.N., Giroldo, A., Glasenhardt, M.-C., Gleason, S., Gliesch, M., Goldberg, E., Göldel, B., Gonzalez-Akre, E., Gonzalez-Andujar, J.L., González-Melo, A., González-Robles, A., Graae, B.J., Granda, E., Graves, S., Green, W.A., Gregor, T., Gross, N., Guerin, G.R., Günther, A., Gutiérrez, A.G., Haddock, L., Haines, A., Hall, J., Hambuckers, A., Han, W., Harrison, S.P., Hattingh, W., Hawes, J.E., He, T., He, P., Heberling, J.M., Helm, A., Hempel, S., Hentschel, J., Hérault, B., Hereş, A.-M., Herz, K., Heuertz, M., Hickler, T., Hietz, P., Higuchi, P., Hipp, A.L., Hirons, A., Hock, M., Hogan, J.A., Holl, K., Honnay, O., Hornstein, D., Hou, E., Hough-Snee, N., Hovstad, K.A., Ichie, T., Igić, B., Illa, E., Isaac, M., Ishihara, M., Ivanov, L., Ivanova, L., Iversen, C.M., Izquierdo, J., Jackson, R.B., Jackson, B., Jactel, H., Jagodzinski, A.M., Jandt, U., Jansen, S., Jenkins, T., Jentsch, A., Jespersen, J.R.P., Jiang, G.-F., Johansen, J.L., Johnson, D., Jokela, E.J., Joly, C.A., Jordan, G.J., Joseph, G.S., Junaedi, D., Junker, R.R., Justes, E., Kabzems, R., Kane, J., Kaplan, Z., Kattenborn, T., Kavelenova, L., Kearsley, E., Kempel, A., Kenzo, T., Kerkhoff, A., Khalil, M.I., Kinlock, N.L., Kissling, W.D., Kitajima, K., Kitzberger, T., Kjøller, R., Klein, T., Kleyer, M., Klimešová, J., Klipel, J., Kloeppel, B., Klotz, S., Knops, J.M.H., Kohyama, T., Koike, F., Kollmann, J., Komac, B., Komatsu, K., König, C., Kraft, N.J.B., Kramer, K., Kreft, H., Kühn, I., Kumarathunge, D., Kuppler, J., Kurokawa, H., Kurosawa, Y., Kuyah, S., Laclau, J.-P., Lafleur, B., Lallai, E., Lamb, E., Lamprecht, A., Larkin, D.J., Laughlin, D., Bagousse-Pinguet, Y.L., Maire, G. le, Roux, P.C. le, Roux, E. le, Lee, T., Lens, F., Lewis, S.L., Lhotsky, B., Li, Y., Li, X., Lichstein, J.W., Liebergesell, M., Lim, J.Y., Lin, Y.-S., Linares, J.C., Liu, C., Liu, D., Liu, U., Livingstone, S., Llusià, J., Lohbeck, M., López-García, Á., Lopez-Gonzalez, G., Lososová, Z., Louault, F., Lukács, B.A., Lukeš, P., Luo, Y., Lussu, M., Ma, S., Pereira, C.M.R., Mack, M., Maire, V., Mäkelä, A., Mäkinen, H., Malhado, A.C.M., Mallik, A., Manning, P., Manzoni, S., Marchetti, Z., Marchino, L., Marcilio-Silva, V., Marcon, E., Marignani, M., Markesteijn, L., Martin, A., Martínez-Garza, C., Martínez-Vilalta, J., Mašková, T., Mason, K., Mason, N., Massad, T.J., Masse, J., Mayrose, I., McCarthy, J., McCormack, M.L., McCulloh, K., McFadden, I.R., McGill, B.J., McPartland, M.Y., Medeiros, J.S., Medlyn, B., Meerts, P., Mehrabi, Z., Meir, P., Melo, F.P.L., Mencuccini, M., Meredieu, C., Messier, J., Mészáros, I., Metsaranta, J., Michaletz, S.T., Michelaki, C., Migalina, S., Milla, R., Miller, J.E.D., Minden, V., Ming, R., Mokany, K., Moles, A.T., Molnár, A., Molofsky, J., Molz, M., Montgomery, R.A., Monty, A., Moravcová, L., Moreno-Martínez, A., Moretti, M., Mori, A.S., Mori, S., Morris, D., Morrison, J., Mucina, L., Mueller, S., Muir, C.D., Müller, S.C., Munoz, F., Myers-Smith, I.H., Myster, R.W., Nagano, M., Naidu, S., Narayanan, A., Natesan, B., Negoita, L., Nelson, A.S., Neuschulz, E.L., Ni, J., Niedrist, G., Nieto, J., Niinemets, Ü., Nolan, R., Nottebrock, H., Nouvellon, Y., Novakovskiy, A., Nystuen, K.O., O'Grady, A., O'Hara, K., O'Reilly-Nugent, A., Oakley, S., Oberhuber, W., Ohtsuka, T., Oliveira, R., Öllerer, K., Olson, M.E., Onipchenko, V., Onoda, Y., Onstein, R.E., Ordonez, J.C., Osada, N., Ostonen, I., Ottaviani, G., Otto, S., Overbeck, G.E., Ozinga, W.A., Pahl, A.T., Paine, C.E.T., Pakeman, R.J., Papageorgiou, A.C., Parfionova, E., Pärtel, M., Patacca, M., Paula, S., Paule, J., Pauli, H., Pausas, J.G., Peco, B., Penuelas, J., Perea, A., Peri, P.L., Petisco-Souza, A.C., Petraglia, A., Petritan, A.M., Phillips, O.L., Pierce, S., Pillar, V.D., Pisek, J., Pomogaybin, A., Poorter, H., Portsmuth, A., Poschlod, P., Potvin, C., Pounds, D., Powell, A.S., Power, S.A., Prinzing, A., Puglielli, G., Pyšek, P., Raevel, V., Rammig, A., Ransijn, J., Ray, C.A., Reich, P.B., Reichstein, M., Reid, D.E.B., Réjou-Méchain, M., Dios, V.R. de, Ribeiro, S., Richardson, S., Riibak, K., Rillig, M.C., Riviera, F., Robert, E.M.R., Roberts, S., Robroek, B., Roddy, A., Rodrigues, A.V., Rogers, A., Rollinson, E., Rolo, V., Römermann, C., Ronzhina, D., Roscher, C., Rosell, J.A., Rosenfield, M.F., Rossi, C., Roy, D.B., Royer-Tardif, S., Rüger, N., Ruiz-Peinado, R., Rumpf, S.B., Rusch, G.M., Ryo, M., Sack, L., Saldaña, A., Salgado-Negret, B., Salguero-Gomez, R., Santa-Regina, I., Santacruz-García, A.C., Santos, J., Sardans, J., Schamp, B., Scherer-Lorenzen, M., Schleuning, M., Schmid, B., Schmidt, M., Schmitt, S., Schneider, J.V., Schowanek, S.D., Schrader, J., Schrodt, F., Schuldt, B., Schurr, F., Garvizu, G.S., Semchenko, M., Seymour, C., Sfair, J.C., Sharpe, J.M., Sheppard, C.S., Sheremetiev, S., Shiodera, S., Shipley, B., Shovon, T.A., Siebenkäs, A., Sierra, C., Silva, V., Silva, M., Sitzia, T., Sjöman, H., Slot, M., Smith, N.G., Sodhi, D., Soltis, P., Soltis, D., Somers, B., Sonnier, G., Sørensen, M.V., Sosinski, E.E., Soudzilovskaia, N.A., Souza, A.F., Spasojevic, M., Sperandii, M.G., Stan, A.B., Stegen, J., Steinbauer, K., Stephan, J.G., Sterck, F., Stojanovic, D.B., Strydom, T., Suarez, M.L., Svenning, J.-C., Svitková, I., Svitok, M., Svoboda, M., Swaine, E., Swenson, N., Tabarelli, M., Takagi, K., Tappeiner, U., Tarifa, R., Tauugourdeau, S., Tavsanoglu, C., Beest, M. te, Tedersoo, L., Thiffault, N., Thom, D., Thomas, E., Thompson, K., Thornton, P.E., Thuiller, W., Tichý, L., Tissue, D., Tjoelker, M.G., Tng, D.Y.P., Tobias, J., Török, P., Tarin, T., Torres-Ruiz, J.M., Tóthmérész, B., Treurnicht, M., Trivellone, V., Trolliet, F., Trotsiuk, V., Tsakalos, J. L., Tsiripidis, I., Tysklind, N., Umehara, T., Usoltsev, V., Vadeboncoeur, M., Vaezi, J., Valladares, F., Vamosi, J., Bodegom, P.M. van, Breugel, M. van, Cleemput, E. V., Weg, M. van de, Merwe, S. van der, Plas, F. van der, Sande, M.T. van der, Kleunen, M. van, Meerbeek, K.V., Vanderwel, M., Vanselow, K.A., Vårhammar, A., Varone, L., Valderrama, M.Y.V., Vassilev, K., Vellend, M., Veneklaas, E.J., Verbeeck, H., Verheyen, K., Vibrans, A., Vieira, I., Villacís, J., Violle, C., Vivek, P., Wagner, K., Waldram, M., Waldron, A., Walker, A.P., Waller, M., Walther, G., Wang, H., Wang, F., Wang, W., Watkins, H., Watkins, J., Weber, U., Weedon, J.T., Wei, L., Weigelt, P., Weiher, E., Wells, A.W., Wellstein, C., Wenk, E., Westoby, M., Westwood, A., White, P.J., Whitten, M., Williams, M., Winkler, D.E., Winter, K., Womack, C., Wright, I.J., Wright, S.J., Wright, J., Pinho, B.X., Ximenes, F., Yamada, T., Yamaji, K., Yanai, R., Yankov, N., Yguel, B., Zanini, K.J., Zanne, A.E., Zelený, D., Zhao, Y.-P., Zheng, Jingming, Zheng, Ji, Ziemińska, K., Zirbel, C.R., Zizka, G., Zo-Bi, I.C., Zotz, G., Wirth, C., 2020. TRY plant trait database – enhanced coverage and open access. Glob. Change Biol. 26, 119–188. https://doi.org/10.1111/gcb.14904.

Keck, F., 2023. Phylosignal. Exploring the Phylogenetic Signal in Continuous Traits. https://CRAN.R-project.org/package=phylosignal.

Kenis, J.D., Silvente, S.T., Trippi, V.S., 1985. Nitrogen metabolism and senescence-associated changes during growth of carnation flowers. Physiol. Plant. 65, 455–459. https://doi.org/10.1111/j.1399-3054.1985.tb08673.x.

Kleyer, M., Minden, V., 2015. Why functional ecology should consider all plant organs: An allocation-based perspective. Basic Appl. Ecol. 16, 1–9. https://doi.org/10.1016/j.baae.2014.11.002.

Lanuza, J.B., Rader, R., Stavert, J., Kendall, L.K., Saunders, M.E., Bartomeus, I., 2023. Covariation among reproductive traits in flowering plants shapes their interactions with pollinators. Funct. Ecol. 37, 2072–2084. https://doi.org/10.1111/1365-2435.14340.

Lefcheck, J.S., Bastazini, V. a G., Griffin, J.N., 2015. Choosing and using multiple traits in functional diversity research. Environ. Conserv. 42, 104–107. https://doi.org/10.1017/S0376892914000307.

Łubek, A., Kukwa, M., Czortek, P., Jaroszewicz, B., 2019. Lichenicolous fungi are more specialized than their lichen hosts in primeval forest ecosystems, Białowieża Forest, northeast Poland. Fungal Ecol. 42, 100866 https://doi.org/10.1016/j.funeco.2019.100866.

Maitner, B.S., Boyle, B., Casler, N., Condit, R., Donoghue II, J., Durán, S.M., Guaderrama, D., Hinchliff, C.E., Jørgensen, P.M., Kraft, N.J.B., McGill, B., Merow, C., Morueta-Holme, N., Peet, R.K., Sandel, B., Schildhauer, M., Smith, S.A., Svenning, J.-C., Thiers, B., Violle, C., Wiser, S., Enquist, B.J., 2018. The bien r package: a tool to access the Botanical Information and Ecology Network (BIEN) database. Methods Ecol. Evol. 9, 373–379. https://doi.org/10.1111/2041-210X.12861.

Martin, A.R., Doraisami, M., Thomas, S.C., 2018. Global patterns in wood carbon concentration across the world's trees and forests. Nat. Geosci. 11, 915–920. https://doi.org/10.1038/s41561-018-0246-x.

McMann, N., Peichel, A., Savage, J.A., 2022. Early spring flowers rely on xylem hydration but are not limited by stem xylem conductivity. New Phytol. 233, 838–850. https://doi.org/10.1111/nph.17782.

Mueller, K.E., Eissenstat, D.M., Hobbie, S.E., Oleksyn, J., Jagodzinski, A.M., Reich, P.B., Chadwick, O.A., Chorover, J., 2012. Tree species effects on coupled cycles of carbon, nitrogen, and acidity in mineral soils at a common garden experiment. Biogeochemistry 111, 601–614. https://doi.org/10.1007/s10533-011-9695-7.

Paglia, I., Pinto, A.R., Amorim, F.W., Arceo-Gómez, G., Freitas, L., 2023. Intra-individual floral variation improves male fitness in a hummingbird-pollinated species. Flora 302, 152270. https://doi.org/10.1016/j.flora.2023.152270.

Paź-Dyderska, S., Dyderski, M.K., Nowak, K., Jagodziński, A.M., 2020. On the sunny side of the crown – quantification of intra-canopy SLA variation among 179 taxa. For. Ecol. Manag. 472, 118254 https://doi.org/10.1016/j.foreco.2020.118254.

Paź-Dyderska, S., Żytkowiak, R., Jagodziński, A.M., 2022. Intra- and interspecific variability of non-structural carbohydrates and phenolic compounds in flowers of 70 temperate trees and shrubs. Forests 13, 1256. https://doi.org/10.3390/f13081256.

Perez, T.M., Valverde-Barrantes, O., Bravo, C., Taylor, T.C., Fadrique, B., Hogan, J.A., Pardo, C.J., Stroud, J.T., Baraloto, C., Feeley, K.J., 2019. Botanic gardens are an untapped resource for studying the functional ecology of tropical plants. Philos. Trans. R. Soc. B Biol. Sci. 374, 20170390. https://doi.org/10.1098/rstb.2017.0390.

Petruzzellis, F., Palandrani, C., Savi, T., Alberti, R., Nardini, A., Bacaro, G., 2017. Sampling intraspecific variability in leaf functional traits: Practical suggestions to maximize collected information. Ecol. Evol. 7, 11236–11245. https://doi.org/10.1002/ece3.3617.

Pyšek, P., Manceur, A.M., Alba, C., McGregor, K.F., Pergl, J., Štajerová, K., Chytrý, M., Danihelka, J., Kartesz, J., Klimešová, J., Lučanová, M., Moravcová, L., Nishino, M., Sádlo, J., Suda, J., Tichý, L., Kühn, I., 2015. Naturalization of central European plants in North America: species traits, habitats, propagule pressure, residence time. Ecology 96, 762–774. https://doi.org/10.1890/14-1005.1.

R Core Team, 2023. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Revell, L.J., 2020. phytools: Phylogenetic Tools for Comparative Biology (and Other Things). https://github.com/liamrevell/phytools.

Roddy, A.B., Brodersen, C.R., Dawson, T.E., 2016. Hydraulic conductance and the maintenance of water balance in flowers. Plant Cell Environ. 39, 2123–2132. https://doi.org/10.1111/pce.12761.

Roddy, A.B., Jiang, G.-F., Cao, K., Simonin, K.A., Brodersen, C.R., 2019. Hydraulic traits are more diverse in flowers than in leaves. New Phytol. 223, 193–203. https://doi.org/10.1111/nph.15749.

Roddy, A.B., Martínez-Perez, C., Teixido, A.L., Cornelissen, T.G., Olson, M.E., Oliveira, R.S., Silveira, F.A.O., 2021. Towards the flower economics spectrum. New Phytol. 229, 665–672. https://doi.org/10.1111/nph.16823.

Rozendaal, D.M.A., Hurtado, V.H., Poorter, L., 2006. Plasticity in leaf traits of 38 tropical tree species in response to light; relationships with light demand and adult stature. Funct. Ecol. 20, 207–216. https://doi.org/10.1111/j.1365-2435.2006.01105.x.

Seth, M.K., 2003. Trees and their economic importance. Bot. Rev. 69, 321–376. https://doi.org/10.1663/0006-8101(2004)069[0321:TATEI]2.0.CO;2.

Stone, G.N., Willmer, P., Rowe, J.A., 1998. Partitioning of Pollinators During Flowering in an African *Acacia* community. Ecology 79, 2808–2827. https://doi.org/10.1890/0012-9658(1998)079[2808:POPDFI]2.0.CO;2.

Svensson, L., 1992. Estimates of hierarchical variation in flower morphology in natural populations of *Scleranthus annuus* (Caryophyllaceae), an inbreeding annual. Plant Syst. Evol. 180, 157–180. https://doi.org/10.1007/BF00941149.

Trocha, L.K., Kałucka, I., Stasińska, M., Nowak, W., Dabert, M., Leski, T., Rudawska, M., Oleksyn, J., 2012. Ectomycorrhizal fungal communities of native and non-native *Pinus* and *Quercus* species in a common garden of 35-year-old trees. Mycorrhiza 22, 121–134. https://doi.org/10.1007/s00572-011-0387-x.

Wickham, H., Chang, W., Henry, L., Pedersen, T.L., Takahashi, K., Wilke, C., Woo, K., Yutani, H., 2020a. ggplot2: Create Elegant Data Visualisations Using the Grammar of Graphics. https://ggplot2.tidyverse.org.

Wickham, H., Francois, R., Henry, L., Müller, K., 2020b. dplyr: A Grammar of Data Manipulation. https://dplyr.tidyverse.org.

Williams, J.L., Conner, J.K., 2001. Sources of phenotypic variation in floral traits in wild radish, *Raphanus raphanistrum* (Brassicaceae). Am. J. Bot. 88, 1577–1581. https://doi.org/10.2307/3558401.

Zhang, C., Li, J., Willis, C.G., Ma, Z., 2020. Among-population variation in seed mass for 190 Tibetan plant species: Phylogenetic pattern and ecological correlates. Glob. Ecol. Conserv. 23, e01163 https://doi.org/10.1016/j.gecco.2020.e01163.

Zhang, F.-P., Yang, Y.-J., Yang, Q.-Y., Zhang, W., Brodribb, T.J., Hao, G.-Y., Hu, H., Zhang, S.-B., 2017. Floral Mass per Area and Water Maintenance Traits Are Correlated with Floral Longevity in *Paphiopedilum* (Orchidaceae). Front. Plant Sci. 8, 501. https://doi.org/10.3389/fpls.2017.00501.

Żywiec, M., Delibes, M., Fedriani, J.M., 2012. Microgeographical, inter-individual, and intra-individual variation in the flower characters of Iberian pear *Pyrus bourgaeana* (Rosaceae). Oecologia 169, 713–722. https://doi.org/10.1007/s00442-011-2232-5.

Publikacja 2.

Paź-Dyderska S., Żytkowiak R., Jagodziński A.M. 2022. Intra- and Interspecific Variability of Non-Structural Carbohydrates and Phenolic Compounds in Flowers of 70 Temperate Trees and Shrubs. Forests 13, 1256. https://doi.org/10.3390/f13081256

Impact Factor 5-letni (2023): 2,7

Punktacja MNiSW (2024): 100

forests

MDPI

Article

Intra- and Interspecific Variability of Non-Structural Carbohydrates and Phenolic Compounds in Flowers of 70 Temperate Trees and Shrubs

Sonia Paź-Dyderska [1,*], Roma Żytkowiak [1] and Andrzej M. Jagodziński [1,2]

[1] Institute of Dendrology, Polish Academy of Sciences, Parkowa 5, 62-035 Kórnik, Poland
[2] Department of Game Management and Forest Protection, Faculty of Forestry and Wood Technology, Poznań University of Life Sciences, Wojska Polskiego 71c, 60-625 Poznań, Poland
* Correspondence: sdyderska@man.poznan.pl; Tel.: +48-61-8170-033; Fax: +48-61-8170-166

Abstract: (1) The focus on floral functional traits and their variability has been significantly lower than when compared to other plant organs. Here, we focused on the variability of four novel floral chemical traits. We aimed to assess the level of interspecific variability of total non-structural carbohydrates (TNC) and total phenolic compounds (TPh) in the flowers of woody species. (2) We collected data on 70 species of temperate trees and shrubs. We also assessed the intraspecific level of variability by collecting flowers from the high-light and low-light parts of the crown. (3) We found a phylogenetic signal in the variability of starch and TPh. We did not observe statistically significant differences or biologically significant trends between the high-light and low-light parts of the crown. We detected a low impact of light availability on the intraspecimen variability of the TNC and TPh contents. (4) Low intraspecimen variability allows for a more reliable extrapolation of measurements in cases of interspecific comparisons and can be used to better describe the reproductive strategies of different woody species.

Keywords: common garden; floral functional traits; intraspecimen variability; reproductive processes; soluble carbohydrates; woody species

check for updates

Citation: Paź-Dyderska, S.; Żytkowiak, R.; Jagodziński, A.M. Intra- and Interspecific Variability of Non-Structural Carbohydrates and Phenolic Compounds in Flowers of 70 Temperate Trees and Shrubs. *Forests* **2022**, *13*, 1256. https://doi.org/10.3390/f13081256

Received: 7 June 2022
Accepted: 4 August 2022
Published: 9 August 2022

1. Introduction

So far, the focus on floral functional traits has been significantly lower compared to other plant organs [1]. Searches for studies on the variability of leaf, seed, and stem functional traits with Google Scholar have provided 293,000, 258,000, and 295,000 results, respectively. Interestingly, there were only one-third as many results for a search regarding flower functional trait variability (i.e., 85,000). The limited temporal availability of flowers in the vegetative season [2], together with their robust morphological diversity [3], may explain why flowers are less frequently studied than other organs. Yet, such a disproportion highlights the need to fill the gaps in our understanding of the traits associated with the flowering strategies of species. Although, in the last decade, more studies on floral traits and how to collect such data have emerged (e.g., flower economics spectrum proposed by Roddy et al. [1]), there is still uncertainty about the intraspecific (including intraspecimen) level of variability of the traits. This is particularly important when taking into consideration that floral traits can be even more functionally diverse than foliar traits [4]. Since trait measurements are often shared via publicly available databases [5,6] and subsequently extrapolated to other specimens representing a given species [7–9], a better understanding of the intraspecific variability of those traits has significant implications for further research that compiles data into meta-analyses [10].

One of the most important aspects of flower biology and ecology is flower contents of the substances responsible for attracting pollinators and deterring herbivores [11]. Naturally, there is a whole range of different chemical and mechanical ways that a plant can use to defend itself [12] or to attract pollinators [13]. Here, we wanted to focus on some of the chemical ways to attract and deter. To attract pollinators and predators feeding on florivores, plants can invest in carbohydrates located, e.g., in pollen and nectar [14]. As a chemical defense against florivores, plants can invest in total phenolic compounds (TPh) [15]. The attracting and deterring strategies, to a considerable extent, evolved as responses to the availability of given kinds of pollinators and herbivores [16–18]. Therefore, the content of carbohydrates and TPh can be assessed as an evolutionary adaptation. As previous studies already detected a phylogenetic signal in the distribution of traits [19,20], phylogenetic signals in the distribution of carbohydrates and TPh contents can also potentially exist. Therefore, carbohydrates and TPh may be used to compare the plant–animal interactions among species but also (while measured at an individual level) to study how the plant invests the given resources into different parts of the crown. Although their meaning is crucial for reproductive processes, the interspecific and intraspecimen variability of the described compounds is still poorly known.

We aimed to assess the level of interspecific variability of soluble carbohydrates, starch, and TPh in the flowers of woody species. We hypothesized that (H1) the interspecific variability of those parameters is correlated with phylogenesis. We assumed that phylogenetically related species show similar values of the parameters studied and therefore represent similar life strategies [21]. We also aimed to assess the intraspecimen levels of variability of the soluble carbohydrates, starch, and TPh contents. We hypothesized that (H2) flowers collected from the sunny (high-light) and shaded (low-light) parts of the crown vary in terms of the soluble carbohydrates, starch, and TPh contents and that flowers collected from high-light will show higher values of those metabolites [22,23]. We assumed that the exposure of flowers to light and heat correlates with a better supply of defense compounds, as similar patterns have been revealed for leaves [22].

2. Materials and Methods

2.1. Study Site

We conducted our study in the Kórnik Arboretum (Western Poland; 52.2448° N, 17.0969° E, 75 m ASL). The Arboretum was founded in the 19th century and consists of a robust collection of ca. 3500 woody taxa, including numerous mature specimens of rare species from all the Northern Hemisphere continents. Plant age is a crucial constraint for flower studies, as for some taxa they take several decades to start reproductive processes, such as blooming or producing fruits. Therefore, Kórnik Arboretum is a suitable location for comparing a wide group of species occurring in a relatively small area. However, the Arboretum was not originally planned to conduct scientific research, and for this reason, we now face some drawbacks derived from an inhomogeneous design connected with the occurrence of a high number of taxa but usually not replicated. Yet, taking into consideration that, in this study, we try to describe novel traits of a high number of woody species, we consider that the Arboretum is an excellent place to conduct the study. In a previous study conducted in the Kórnik Arboretum, the authors successfully collected the data to assess the intraspecific variability of a specific leaf area of 179 taxa [24], and we think this is a reasonable argument for considering the Arboretum as a valuable study site to conduct research in the field of functional ecology.

The mean growing season length in the study location is 220 days, the mean annual precipitation is 544 mm, and the mean annual temperature is 8.3 °C [25]. The Arboretum is not spatially extensive; thus, the environmental conditions, including climate and soil type, are very similar for all the specimens analyzed in our study. Due to the temporary availability of the flowers and the time-consuming procedure of analyzing the samples, we collected samples from 70 angiosperm species of trees and shrubs representing 27 families. We collected data from one specimen per species, as we wanted to include as many species as possible in our study. On the other hand, the availability of numerous specimens representing the same taxa varies throughout the collection and has its limits. This means that sometimes there was only one flowering specimen of a given taxon of interest. For this reason, we decided not to collect data from more specimens even when possible to maintain a fixed sample size for each species studied.

2.2. Data Collection

We collected data from April to July 2021. We decided to collect fully developed flowers with no signs of herbivory, pathogenic infections or mechanical damage, as has been suggested for leaves [26]. There is a lack of explicit protocols for measuring many floral traits, but similar sampling designs, including data collection for floral traits on species with limited replications, e.g., in botanical gardens, have been done before [4,27,28]. Thus, we decided to follow some of the previous ideas from the field, e.g., to include the pedicel and peduncle. Additionally, in cases of species such as *Corylus* spp. or *Quercus* sp., with small, inconspicuous flowers, we included the whole inflorescences together with the pedicel/peduncle, because we wanted to include all the showy floral structures, as their main convergent function is to attract pollinators [27]. We collected floral organs at the peak flowering time [28]. To assess not only the interspecific but also the intraspecific levels of variability, we collected at least ten flowers (or inflorescences) from the sunniest and ten flowers from the most shaded parts of the crown with a 6-m-long pole pruner. However, there were some exceptions, i.e., we collected fewer flowers of species producing very big flowers (e.g., *Magnolia tripetala* (L.) L.), as we did not want to harm the rare specimens. We selected the flowers for the study based on qualitative observations with no measurements of the light availability, similar to Paź-Dyderska et al. [24]. As a result, we obtained two samples per species from each variant of the study, i.e., high-light and low-light. We put the harvested flowers in envelopes to minimize the risk of losing fragile parts of the plant material. Then, all flowers were dried in an oven with forced air circulation at 65 °C (ULE 600 and UF450, Memmert GmbH + Co. KG, Regensburg, Germany) to a constant mass using the same methodology as in numerous studies previously carried out in our laboratory [29–31].

2.3. Chemical Analysis

We analyzed all chemical compounds as dried flower tissue ground in a Mikro-Feinmühle-Culatti mill (IKA Labortechnik, Staufen im Breisgau, Germany). We assessed the contents of total non-structural carbohydrates (TNC; soluble carbohydrates and starch) as proposed by Hansen and Møller [32] and Haissig and Dickson [33]. We assayed soluble carbohydrates in methanol–chloroform–water extracts (λ = 625 nm), following a color reaction with anthrone. We presented TNC results as a % of the dry mass. The starch analysis consisted of its transformation into glucose, with amyloglucosidase and oxidation using the peroxidase–glucose oxidase complex. We measured the concentrations of starch at λ = 450 nm following the reaction with dianisidine. We measured the TPh content (λ = 660 nm) with Folin and Ciocalteu's Phenol Reagent (SIGMA F-9252) using the methodology of Johnson and Schaal [34] with the modification of Singleton and Rossi [35]. The results we obtained were expressed in units of µM of a chlorogenic acid g^{-1} dry mass. We followed the methodology of previous studies on chemical compositions [36,37].

2.4. Data Analysis

We analyzed our data using R software (R Core Team, 2021). We processed the data using the *dplyr* package [38] and visualized them with the *ggplot2* package [39]. We expressed interspecific variability using the coefficient of variation (CV). To assess the impact of the light variant on the content of a given chemical compound, we performed a phylogenetic paired *t*-test using the *phyl.pairedttest* function from the *phytools* package [40]. This way, we could assess the eventual impacts of the canopy position on the contents of the chemical compounds studied in a given sample.

To verify whether the interspecific variability of the soluble carbohydrates, starch, and TPh in the flowers of woody species is correlated with the phylogenesis of the species, we used a phylogenetic tree for the species studied obtained from the *V.PhyloMaker* package [41]. Then, we assessed the C mean, Blomberg's K, K.star, and Lambda phylogenetic correlation coefficients using the *Phylosignal* package [42–44].

3. Results

The mean values of the soluble carbohydrates in the flowers (Figure 1 and Table 1) of the species studied ranged from 3.206% (*Ailanthus altissima* (Mill.) Swingle) to 27.039% (*Catalpa bignonioides* Walter). The CV for soluble carbohydrates was 44.4%. For starch, the mean values ranged from 0.739% (*Viburnum sieboldii* Miq.) to 10.323% (*Asimina triloba* (L.) Dunal), with a CV of 110.4%. The range of the TNC mean values differed from 3.997% (*A. altissima*) to 27.819% (*C. bignonioides*), and the CV was 41.4%. Lastly, the TPh values ranged from 46.147 (*Laburnum anagyroides* Medik.) to 1085.734 (*Sorbus torminalis* (L.) Crantz) μM of the chlorogenic acid g^{-1} dry mass, with a CV of 70.5%. Generally, the variability was the highest in starch and lowest in the soluble carbohydrates and TNC.

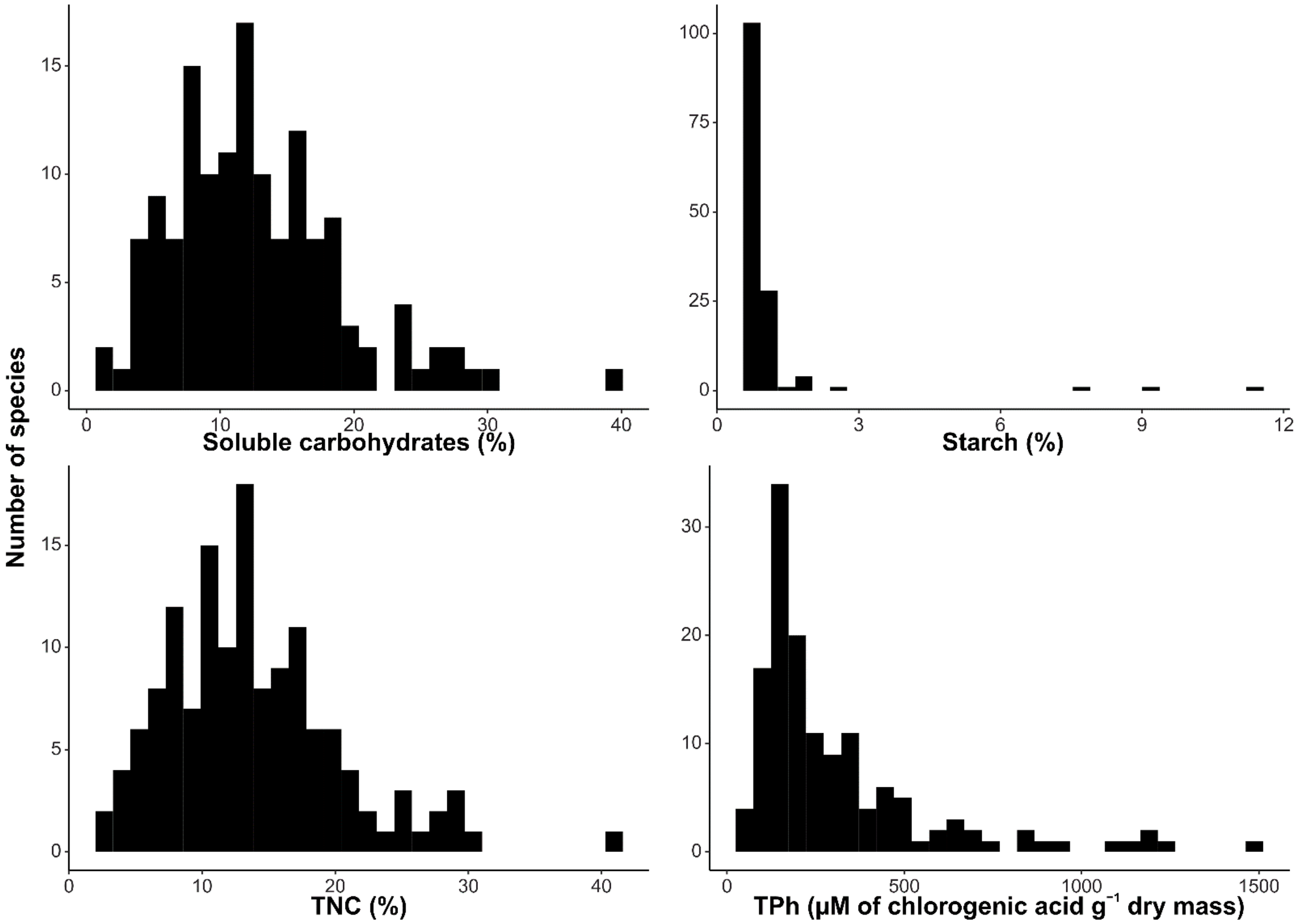


Figure 1. Distribution of the soluble carbohydrates, starch, TNC, and TPh contents for the species studied.

Table 1. Overview of the species studied and their mean soluble carbohydrates, starch, TNC, and TPh values.

Species	Family	Soluble Carbohydrates (%)	Starch (%)	TNC (%)	TPh (μM of Chlorogenic Acid g^{-1} Dry Mass)
Acer pensylvanicum L.	*Sapindaceae*	11.370	0.908	12.278	151.140
Acer pseudoplatanus L.	*Sapindaceae*	9.937	0.784	10.721	462.983
Aesculus glabra Willd.	*Sapindaceae*	16.541	0.947	17.487	148.197
Aesculus hippocastanum L.	*Sapindaceae*	24.097	0.889	24.985	118.706
Aesculus parviflora Walter	*Sapindaceae*	14.290	0.838	15.128	180.177
Aesculus turbinata Blume	*Sapindaceae*	17.239	0.983	18.222	106.805
Ailanthus altissima (Mill.) Swingle	*Simaroubaceae*	3.206	0.791	3.997	163.528
Asimina triloba (L.) Dunal	*Annonaceae*	10.415	10.323	20.738	306.558
Berberis amurensis Rupr.	*Berberidaceae*	14.147	0.849	14.996	199.478
Berberis aquifolium Pursh	*Berberidaceae*	9.477	0.813	10.290	308.063
Berberis julianae C.K.Schneid.	*Berberidaceae*	18.214	0.829	19.043	268.745
Calycanthus fertilis Walter	*Calycanthaceae*	10.683	1.875	12.558	411.063
Carpinus orientalis Mill.	*Betulaceae*	17.830	0.945	18.774	264.294
Castanea sativa Mill.	*Fagaceae*	12.040	0.846	12.885	294.083
Catalpa bignonioides Walter	*Bignoniaceae*	27.039	0.780	27.819	316.005
Cercidiphyllum japonicum Siebold & Zucc.	*Cercidiphyllaceae*	3.822	0.895	4.717	897.379
Cercis chinensis Bunge	*Fabaceae*	15.134	0.869	16.003	140.805
Cornus florida L.	*Cornaceae*	10.661	0.894	11.555	132.362
Cornus mas L.	*Cornaceae*	16.460	0.827	17.287	391.879
Cornus officinalis Siebold & Zucc.	*Cornaceae*	12.840	0.873	13.714	320.996
Corylopsis platypetala Rehder & E.H.Wilson	*Hamamelidaceae*	9.597	0.829	10.426	300.624
Corylopsis sinensis Hemsl.	*Hamamelidaceae*	11.029	0.916	11.944	278.399
Corylus avellana L.	*Betulaceae*	5.492	0.787	6.279	177.459
Corylus colurnoides C.K.Schneid.	*Betulaceae*	5.604	0.876	6.481	207.546
Crataegus holmesiana Ashe	*Rosaceae*	14.759	0.785	15.544	638.765
Crataegus submollis Sarg.	*Rosaceae*	13.385	0.860	14.244	253.148
Cydonia oblonga Mill.	*Rosaceae*	16.109	0.894	17.003	410.986
Davidia involucrata Baill.	*Nyssaceae*	13.765	0.902	14.667	405.669
Euonymus atropurpureus Jacq.	*Celastraceae*	23.851	0.816	24.667	289.730
Exochorda korolkowii Lavallée	*Rosaceae*	8.334	0.885	9.219	102.092
Exochorda racemosa (Lindl.) Rehder	*Rosaceae*	5.739	0.917	6.656	180.500
Forsythia giraldiana Lingelsh.	*Oleaceae*	15.786	0.804	16.590	170.925
Fothergilla major (Sims) Lodd.	*Hamamelidaceae*	3.338	0.890	4.228	353.830
Halesia carolina L.	*Styracaceae*	7.710	0.979	8.689	168.546
Hamamelis mollis Oliv.	*Hamamelidaceae*	5.127	0.961	6.087	288.367
Jasminum fruticans L.	*Oleaceae*	20.717	1.823	22.540	224.298
Kolkwitzia amabilis Graebn.	*Caprifoliaceae*	15.240	0.815	16.055	192.775
Laburnum anagyroides Medik.	*Fabaceae*	14.179	0.899	15.078	46.147
Lonicera standishii Jacques	*Caprifoliaceae*	13.208	0.899	14.106	149.106
Magnolia kobus DC.	*Magnoliaceae*	10.648	0.880	11.529	106.566
Magnolia stellata (Siebold & Zucc.) Maxim.	*Magnoliaceae*	6.634	0.855	7.489	130.447
Magnolia tripetala (L.) L.	*Magnoliaceae*	8.162	1.239	9.400	134.390
Malus baccata (L.) Moench	*Rosaceae*	11.795	0.879	12.674	207.765
Malus ×hartwigii Koehne	*Rosaceae*	8.746	0.904	9.650	187.132
Parrotia persica (DC.) C.A.Mey.	*Hamamelidaceae*	5.089	0.852	5.940	394.519
Paulownia tomentosa (Thunb.) Steud.	*Paulowniaceae*	13.154	0.756	13.910	849.438
Prunus incisa Thunb.	*Rosaceae*	9.114	0.823	9.937	128.512
Prunus laurocerasus L.	*Rosaceae*	18.476	0.882	19.358	125.202
Prunus padus L.	*Rosaceae*	22.316	1.146	23.462	576.903
Prunus serrulata Lindl.	*Rosaceae*	15.747	0.859	16.606	160.956
Quercus rubra L.	*Fagaceae*	3.832	0.783	4.615	471.303
Rhododendron luteum Sweet	*Ericaceae*	8.809	0.978	9.787	621.978
Rhus aromatica Aiton	*Anacardiaceae*	11.372	0.935	12.307	430.295

Table 1. *Cont.*

Species	Family	Soluble Carbohydrates (%)	Starch (%)	TNC (%)	TPh (µM of Chlorogenic Acid g^{-1} Dry Mass)
Salix gracilistyla Miq.	*Salicaceae*	6.805	0.921	7.726	187.302
Sambucus siberica Nakai	*Adoxaceae*	5.189	0.772	5.961	161.683
Sorbus aucuparia L.	*Rosaceae*	9.004	0.756	9.760	313.785
Sorbus torminalis (L.) Crantz	*Rosaceae*	8.478	0.743	9.222	1085.734
Spiraea longigemmis Maxim.	*Rosaceae*	19.226	1.335	20.561	677.810
Spiraea media F.Schmidt	*Rosaceae*	14.617	0.840	15.457	488.532
Spiraea ×nudiflora Zabel	*Rosaceae*	25.608	0.896	26.504	526.887
Staphylea pinnata L.	*Staphyleaceae*	11.984	0.950	12.935	97.215
Syringa josikaea J.Jacq. ex Rchb.	*Oleaceae*	19.131	0.850	19.981	802.407
Syringa meyeri C.K.Schneid.	*Oleaceae*	22.174	0.744	22.918	378.130
Syringa vulgaris L.	*Oleaceae*	11.067	0.896	11.963	149.656
Tilia cordata Mill.	*Malvaceae*	13.510	0.773	14.283	414.117
Viburnum carlesii Hemsl. ex Forbes & Hemsl.	*Adoxaceae*	20.033	0.797	20.830	274.190
Viburnum lantana L.	*Adoxaceae*	15.060	0.867	15.928	139.919
Viburnum sieboldii Miq.	*Adoxaceae*	10.450	0.739	11.189	133.098
Weigela florida (Bunge) A.DC.	*Caprifoliaceae*	16.514	0.883	17.397	76.666
Zelkova serrata (Thunb.) Makino	*Ulmaceae*	5.180	4.403	9.583	875.596

The variability of starch and TPh showed phylogenetic signals, while we did not observe a correlation between the soluble carbohydrates and TNC variability levels with the phylogenetic signal. We observed a moderate phylogenetic signal in TPh (Figure 2 and Table 2). The starch content showed a stronger phylogenetic signal; however, this was mainly caused by an outlier observation of *Paulownia tomentosa* (Thunb.) Steud. We did not observe a significant evolutionary signal for soluble carbohydrates or TNC. Although the phylogenetic signal was the strongest for starch, it was not statistically significant due to the strong impact of the outlier. The signal was statistically significant only for TPh.

Table 2. Phylogenetic signals of the soluble carbohydrates, starch, TNC, and TPh represented by the C mean, I, Blomberg's K, K.star, and Lambda phylogenetic correlation coefficients. Statistically significant coefficient values are italicized.

Parameter Studied	Cmean	I	K	K.star	Lambda
Soluble carbohydrates	−0.067	−0.007	0.135	0.143	6.70×10^{-5}
Starch	−0.033	−0.011	0.550	0.567	*1.011*
TNC	−0.051	−0.007	0.138	0.146	6.70×10^{-5}
TPh	*0.207*	0.000	*0.275*	*0.268*	$\mathit{6.78 \times 10^{-1}}$

We did not observe statistically significant differences or biologically significant trends between the high-light and low-light parts of the crown (Table 3 and Figure 3). The phylogenetic mean values of the differences between those two variants of light availability for the soluble carbohydrates, starch, TNC, and TPh were −0.996%, 0.448%, −0.807%, and 51.069 µM of chlorogenic acid g^{-1} dry mass, respectively (Table 3). The minimum difference for the soluble carbohydrates was 0.23% (*Halesia carolina*), <0.01% for starch (e.g., *Castanea sativa* Mill.), 0.18% for TNC (*P. tomentosa*), and 0.49 µM of chlorogenic acid g^{-1} dry mass for TPh (*Tilia cordata* Mill.). The maximum difference value for soluble carbohydrates was 28.80% (*Spiraea × nudiflora* Zabel), 6.98% for starch (*Zelkova serrata* (Thunb.) Makino), 29.05% for TNC (*S. nudiflora*), and 1021.80 µM of chlorogenic acid g^{-1} dry mass for TPh (*Spiraea longigemmis* Maxim.).

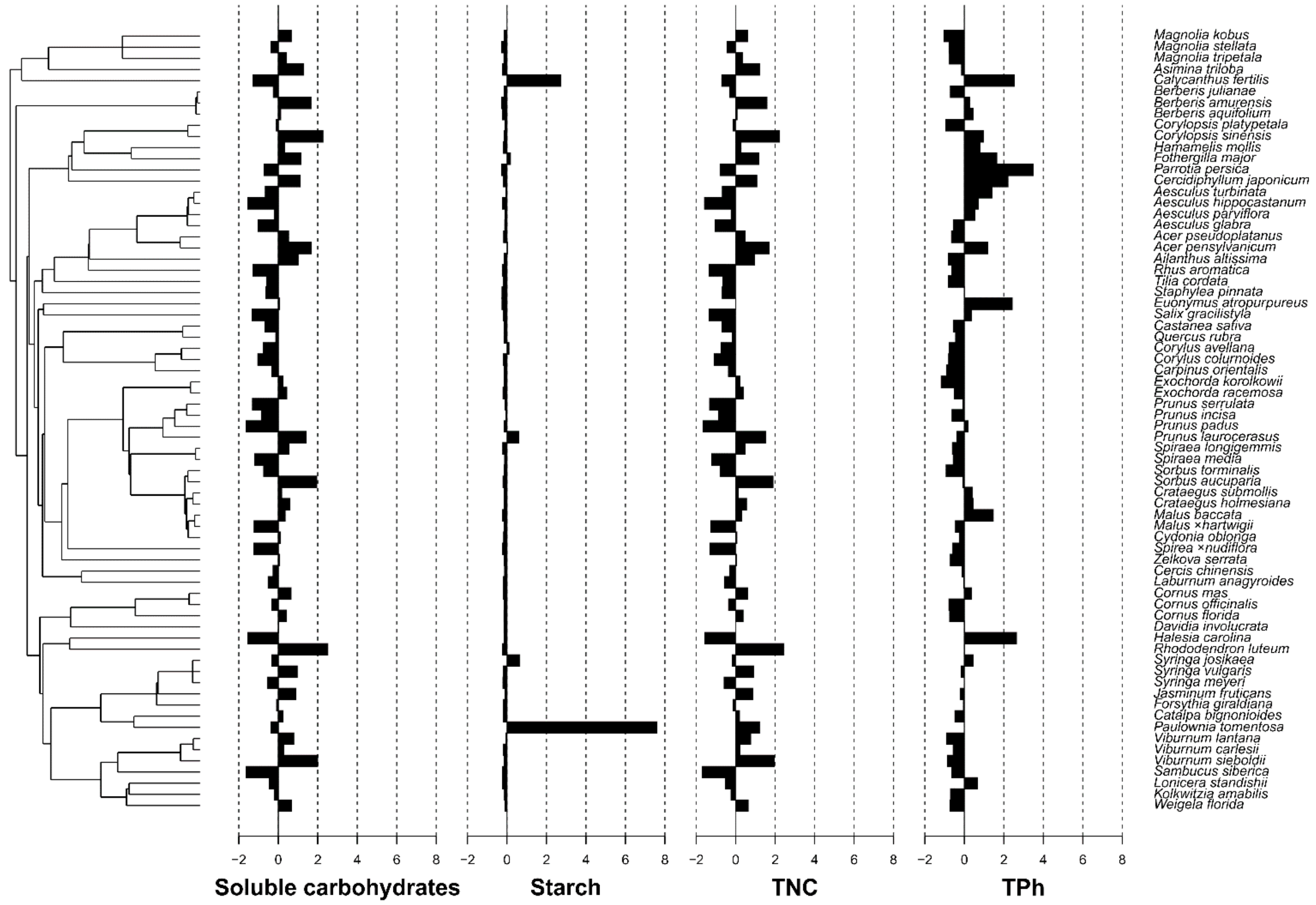


Figure 2. Mean standardized values of soluble carbohydrates, starch, TNC, and TPh for each species. The number zero on the X-axes defines the mean value of each component calculated for all the species. The longer the bar, the greater the difference between the mean value of the trait and the trait value obtained for a particular species.

Table 3. Parameters of phylogenetic paired *t*-tests comparing soluble carbohydrates, starch, TNC, and TPh variability between flowers from high-light and low-light parts of the crown.

	Phylogenetic Mean Difference	95% CI	*t*	*p*-Value
Soluble carbohydrates	−0.996	−2.410, 0.419	−1.379	0.172
Starch	0.448	−0.295, 1.192	1.182	0.241
TNC	−0.807	−2.239, 0.624	−1.106	0.273
TPh	51.069	−172.195, 274.333	0.448	0.655

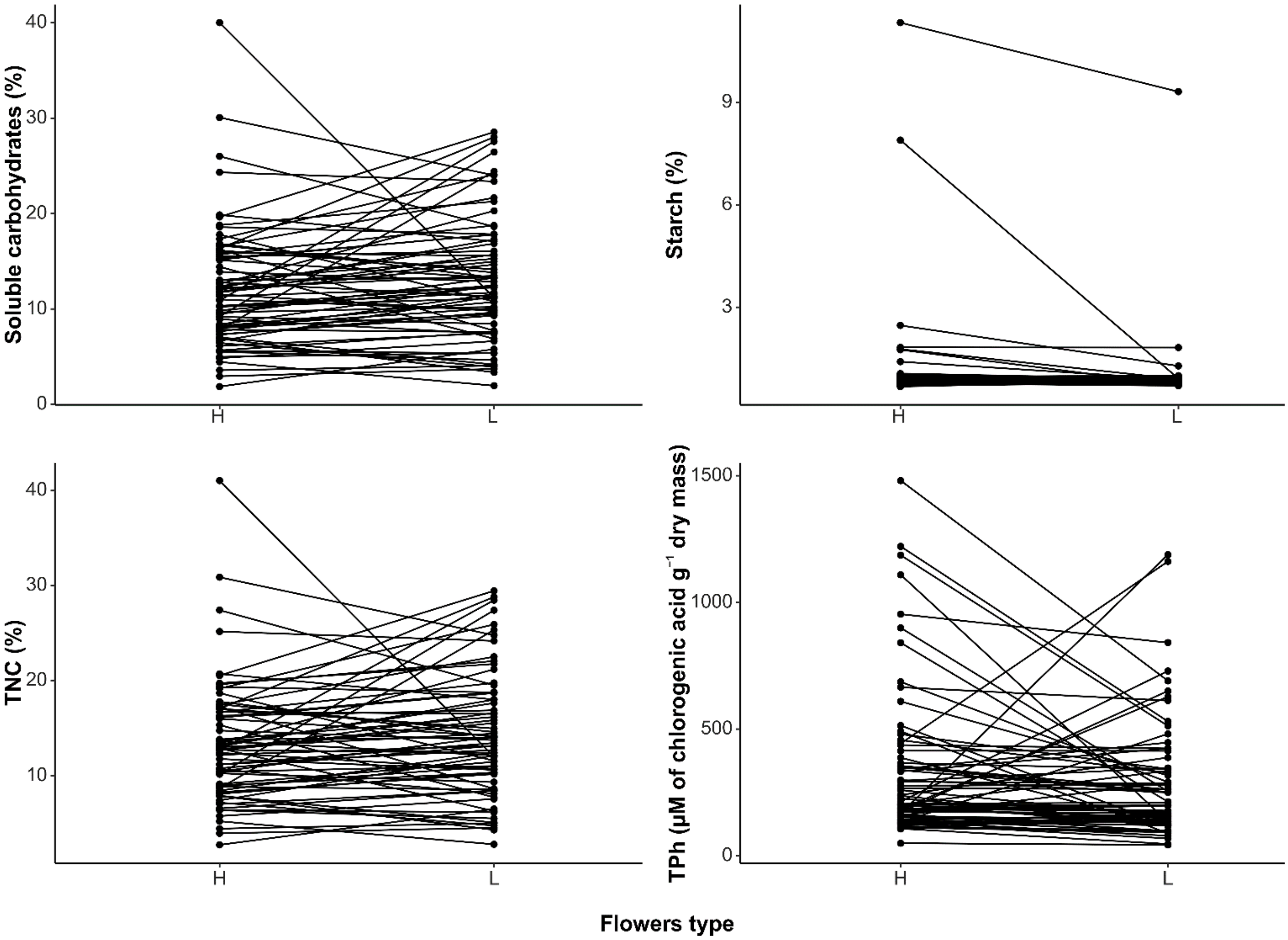


Figure 3. Observed soluble carbohydrates, starch, TNC, and TPh species-wise differences between high-light (H) and low-light (L) parts of the crown. Each line represents the slope of a trait difference for a particular species.

4. Discussion

Our study presents novel data on the variability of flowers in terms of the TNC and TPh contents, which are crucial for a better understanding of the reproductive strategies of plants. Similar studies of chemical contents for flowers are sparse. For example, Chen et al. [45] compared floral scent compounds for three *Styrax* species, but this was focused on a narrow range of taxa. However, analogical research is more developed for other floral traits. Studies regarding floral functional traits often focus on reproductive success and plant–pollinator interactions studied on an interspecific level, considering high floral variability as a form of adaptation to more successful pollination [46]. For example, in the case of well-studied orchids known for their high variability of floral traits, Lussu et al. [47] found that the morphological variability of functional traits related to the fertilization process may constitute a natural barrier preventing the crossing of cooccurring species. Juillet and Scopece [48], based on a review of eight experimental and correlative studies, detected that a high phenotypic variability of orchids probably does not positively affect reproductive success. Generally, we found that previous studies from this field regarded rather narrow groups of species and did not focus on the contents of carbohydrates and TPh in flowers. We also did not find any previous studies focusing on the variability of those traits occurring within individuals. However, it should be highlighted that previous studies have measured numerous pivotal floral traits that we did not include in our study, such as, for example, biomass, size, shape, or color [23]. Therefore, with this study, we contribute to the extension of an already thriving flower-related branch of functional ecology.

In this study, we detected that, among the studied variables, the highest variability occurred in the case of starch, and the lowest in the cases of soluble carbohydrates and TNC. We found no phylogenetic signals for the values of soluble carbohydrates and TNC, but we found that the starch and TPh contents were correlated with phylogenesis. However, only TPh showed a statistically significant correlation with phylogenesis. We assume that not only the presence of outliers could affect our results but also a limited number of species. We analyzed plant materials collected from 70 species, which is a sufficient number for a phylogenetic analysis. The root:shoot ratio [19], specific leaf area [24], variation in seed mass [49], or wood carbon concentration [50] are only some of the examples of the correlation of functional traits with the evolutionary history of species. On the other hand, phylogenetically clustered plants may show higher functional diversity, which can be interpreted as a way to stabilize the coexistence of a set of evolutionarily related species [51]. Thus, the weak phylogenetic signal we detected can be derived from the natural ecological diversity of species within the same family or genus.

We faced some trade-offs at the design stage of our study. Flowering being an ephemeral process that occurs at different times during the growing season prevented us from collecting the data at one point in time (as was possible, for example, with leaves available for months during the vegetative season). Simultaneously, we are aware of the seasonal variability of flowers and their contents in chemical compounds, not only TNC and TPh analyzed in this study. As was detected for other organs (e.g., carbon content increase in aging leaves, as described by Reich and coauthors [52]), there are also seasonal changes in the contents of chemical compounds in flowers [53–55]. However, as indicated by the literature review, our study is one of the first attempts at detecting the potential TNC and TPh contents in flowers for use in functional ecology, and therefore, we consciously decided to skip this type of variability as negligible at this stage of the development of this field of knowledge. Moreover, as detected by Siatka and Kašparová [56], seasonal variations of TPh in flowers of *Bellis perennis* L. showed comparable values throughout the whole growing season, i.e., from spring to autumn. Additionally, we believe that, similar to a previous study by Paź-Dyderska et al. [24], the concept of a common garden design of the study (i.e., numerous species growing in one area with similar climatic conditions) to a certain degree decreases the disadvantages resulting from the abovementioned shortcomings.

We decided to include only one specimen per species to increase the number of species. To our knowledge, the optimum sample size for the study of the intraspecimen variability of flowers has not been assessed yet, but in the case of foliar traits, the most accurate sampling size covers four samples from 10 individuals [57]. Thus, although we are conscious that a higher number of the specimens would better represent the data variability, we collected flowers from singular specimens. This resulted not only from the characteristics of the Arboretum layout, which often includes only one mature specimen of a given species, but also from the time-consuming process of collecting data. Since species flowering periods often overlap and vary from year to year, the harvest of flowers required monitoring the stages of flower development for all species throughout the growing season and waiting for the optimal flowering phase to collect the material for each species. Hence, the collection of flowers takes more time than, e.g., the collection of leaves. Yet, such data can be truly attractive for further use in functional ecology.

The low level of intraspecimen variability and relatively high level of interspecific variability of TNC and TPh can have significant advantages while advocating for the wider use of those parameters as functional traits [58–60]. The low intraspecimen variability that we detected is favorable, as the human decision of which flowers to collect has a lesser impact on the results obtained than the leaves, which, in the case of the specific leaf area, may differ ca. 40% just within one individual [24]. Nevertheless, we should keep in mind that, in this study, we focused only on the concentrations of the chemical compounds, with no focus on their absolute amounts, which vary depending on the flower size. As the flower size can potentially vary from high-light to low-light, it can be difficult to assess the importance of the low intraspecific variability detected. Yet, using concentrations is an efficient way of comparing samples from different crown locations, and we believe that this method provides some valuable insight into the flowering biology of the woody species.

Simultaneously, we showed significant interspecific variability, which is useful while searching for potential differences among species and their flowering strategies. Moreover, the data we provide might be used for modeling plant–animal interactions, as the TNC and TPh are related to the species strategies of attracting pollinators (e.g., a high starch concentration in pollen is related to pollen maturity [61]) or defending from herbivores [15]. Previous studies showing the impact of soluble carbohydrates on the longevity of flowers in the floristic industry indicated the potential for the use of TNC in functional ecology. For example, Monteiro and coauthors revealed that a higher TNC content in potted miniature roses correlated positively with the flower longevity and that injecting the plants with sucrose solution increased the flower longevity by 1.5 days [62]. Ranwala and Miller [63] showed that the postharvest longevity of tulips can be increased up to 18–37%, depending on the treatment, by supplying sucrose and trehalose solutions. In the context of functional ecology, however, the potential of using TNC as a tool to study flower longevity is yet to be explored. The same is true for phenolic compounds, where there is a potential for the use of TPh in studies of plant antifungal strategies. In our study, we measured the total phenolic compound contents, but Petersen [64] highlighted that one of the phenolic compounds, i.e., rosmarinic acid, has important antifungal effects in plants with flowers. Thus, delving into more detailed chemical analyses may lead to broadening the possibilities of using the traits we studied in forthcoming ecological studies. That is why we believe that the incorporation of TNC and TPh into studies on flowering biology and ecology may contribute to a better understanding of the reproductive processes that are crucial for the maintenance of diverse ecosystems.

5. Conclusions

Our results expand the knowledge of the biology and ecology of flowering in woody plants. We provided new, quantitative data on the soluble carbohydrates and TPh contents in flowers of 70 temperate species of trees and shrubs. We showed a weak correlation between their chemical contents and evolutionary history by preparing a phylogenetic tree for the set of species studied. We detected a low impact of the light availability on the intraspecimen variability of the TNC and TPh contents, which highlights the potential of those traits to be used in functional ecology. A low intraspecimen variability is more favorable for intraspecific comparisons and analyses and can be used to better describe the functional differences of flowers and, subsequently, differences in the reproductive strategies of different woody species.

Author Contributions: Conceptualization, S.P.-D. and A.M.J.; methodology, S.P.-D. and A.M.J.; software, S.P.-D.; validation, S.P.-D., A.M.J. and R.Ż.; formal analysis, S.P.-D.; chemical analysis, R.Ż.; investigation, S.P.-D.; data curation, S.P.-D.; writing—original draft preparation, S.P.-D.; writing—review and editing, A.M.J. and R.Ż.; visualization, S.P.-D.; supervision, A.M.J.; project administration, S.P.-D.; and funding acquisition, S.P.-D. All authors have read and agreed to the published version of the manuscript.

Funding: This research was funded by the Institute of Dendrology, Polish Academy of Sciences, Kórnik, Poland, grant number 2021/01/ZB/FBW/00003.

Data Availability Statement: Not available.

Acknowledgments: We are grateful to Kinga Nowak for her help in selecting species suitable for our research. We are thankful to Piotr Karolewski for his consultation regarding the chemical analyses of phenolic compounds. We would like to thank Marcin K. Dyderski for his critical comments on the manuscript.

Conflicts of Interest: The authors declare no conflict of interest.

References

1. Roddy, A.B.; Martínez-Perez, C.; Teixido, A.L.; Cornelissen, T.G.; Olson, M.E.; Oliveira, R.S.; Silveira, F.A.O. Towards the flower economics spectrum. *New Phytol.* **2021**, *229*, 665–672. [CrossRef] [PubMed]
2. Gao, J.; Xiong, Y.-Z.; Huang, S.-Q. Effects of floral sexual investment and dichogamy on floral longevity. *J. Plant Ecol.* **2015**, *8*, 116–121. [CrossRef]
3. van der Niet, T.; Johnson, S. Phylogenetic evidence for pollinator-driven diversification of angiosperms. *Trends Ecol. Evol.* **2012**, *27*, 353–361. [CrossRef]
4. Roddy, A.B.; Jiang, G.-F.; Cao, K.; Simonin, K.A.; Brodersen, C.R. Hydraulic traits are more diverse in flowers than in leaves. *New Phytol.* **2019**, *223*, 193–203. [CrossRef] [PubMed]
5. Kattge, J.; Bönisch, G.; Díaz, S.; Lavorel, S.; Prentice, I.C.; Leadley, P.; Tautenhahn, S.; Werner, G.D.A.; Aakala, T.; Abedi, M.; et al. TRY plant trait database—Enhanced coverage and open access. *Glob. Chang. Biol.* **2020**, *26*, 119–188. [CrossRef] [PubMed]
6. Kleyer, M.; Bekker, R.M.; Knevel, I.C.; Bakker, J.P.; Thompson, K.; Sonnenschein, M.; Poschlod, P.; van Groenendael, J.M.; Klimeš, L.; Klimešová, J.; et al. The LEDA Traitbase: A database of life-history traits of the Northwest European flora. *J. Ecol.* **2008**, *96*, 1266–1274. [CrossRef]
7. Campetella, G.; Chelli, S.; Simonetti, E.; Damiani, C.; Bartha, S.; Wellstein, C.; Giorgini, D.; Puletti, N.; Mucina, L.; Cervellini, M.; et al. Plant functional traits are correlated with species persistence in the herb layer of old-growth beech forests. *Sci. Rep.* **2020**, *10*, 19253. [CrossRef]
8. Dyderski, M.K.; Jagodziński, A.M. Impacts of invasive trees on alpha and beta diversity of temperate forest understories. *Biol. Invasions* **2021**, *23*, 235–252. [CrossRef]
9. Tecco, P.A.; Díaz, S.; Cabido, M.; Urcelay, C. Functional traits of alien plants across contrasting climatic and land-use regimes: Do aliens join the locals or try harder than them? *J. Ecol.* **2010**, *98*, 17–27. [CrossRef]
10. Albert, C.H.; Thuiller, W.; Yoccoz, N.G.; Soudant, A.; Boucher, F.; Saccone, P.; Lavorel, S. Intraspecific functional variability: Extent, structure and sources of variation. *J. Ecol.* **2010**, *98*, 604–613. [CrossRef]
11. Farré-Armengol, G.; Filella, I.; Llusia, J.; Peñuelas, J. Floral volatile organic compounds: Between attraction and deterrence of visitors under global change. *Perspect. Plant Ecol. Evol. Syst.* **2013**, *15*, 56–67. [CrossRef]
12. Gong, B.; Zhang, G. Interactions between plants and herbivores: A review of plant defense. *Acta Ecol. Sin.* **2014**, *34*, 325–336. [CrossRef]
13. Frachon, L.; Stirling, S.A.; Schiestl, F.P.; Dudareva, N. Combining biotechnology and evolution for understanding the mechanisms of pollinator attraction. *Curr. Opin. Biotechnol.* **2021**, *70*, 213–219. [CrossRef]
14. Venjakob, C.; Ruedenauer, F.A.; Klein, A.; Leonhardt, S.D. Variation in nectar quality across 34 grassland plant species. *Plant Biol.* **2021**, *24*, 134–144. [CrossRef] [PubMed]
15. Nakano, S.; Oguro, M.; Itagaki, T.; Sakai, S. Florivory defence: Are phenolic compounds distributed non-randomly within perianths? *Biol. J. Linn. Soc.* **2020**, *131*, 12–25. [CrossRef]
16. Gervasi, D.D.L.; Schiestl, F. Real-time divergent evolution in plants driven by pollinators. *Nat. Commun.* **2017**, *8*, 14691. [CrossRef]
17. Knauer, A.C.; Schiestl, F. The effect of pollinators and herbivores on selection for floral signals: A case study in *Brassica rapa*. *Evol. Ecol.* **2016**, *31*, 285–304. [CrossRef]
18. Strauss, S.Y. Floral characters link herbivores, pollinators, and plant fitness. *Ecology* **1997**, *78*, 1640–1645. [CrossRef]
19. Burns, J.H.; Strauss, S.Y. Effects of competition on phylogenetic signal and phenotypic plasticity in plant functional traits. *Ecology* **2012**, *93*, S126–S137. [CrossRef]
20. Martin, A.R.; Thomas, S.C.; Zhao, Y. Size-dependent changes in wood chemical traits: A comparison of neotropical saplings and large trees. *AoB PLANTS* **2013**, *5*, plt039. [CrossRef]
21. Chanderbali, A.S.; Berger, B.A.; Howarth, D.G.; Soltis, P.S.; Soltis, D.E. Evolving ideas on the origin and evolution of flowers: New perspectives in the genomic era. *Genetics* **2016**, *202*, 1255–1265. [CrossRef]
22. Karolewski, P.; Giertych, M.J.; Żmuda, M.; Jagodziński, A.M.; Oleksyn, J. Season and light affect constitutive defenses of understory shrub species against folivorous insects. *Acta Oecol.* **2013**, *53*, 19–32. [CrossRef]
23. Roddy, A.B. Energy balance implications of floral traits involved in pollinator attraction and water balance. *Int. J. Plant Sci.* **2019**, *180*, 944–953. [CrossRef]
24. Paź-Dyderska, S.; Dyderski, M.K.; Nowak, K.; Jagodziński, A.M. On the sunny side of the crown—Quantification of intra-canopy SLA variation among 179 taxa. *For. Ecol. Manag.* **2020**, *472*, 118254. [CrossRef]
25. Cedro, A.; Iszkuło, G. Do females differ from males of European yew (*Taxus baccata* L.) in dendrochronological analysis? *Tree-Ring Res.* **2011**, *67*, 3–11. [CrossRef]
26. Pérez-Harguindeguy, N.; Díaz, S.; Garnier, E.; Lavorel, S.; Poorter, H.; Jaureguiberry, P.; Bret-Harte, M.S.; Cornwell, W.K.; Craine, J.M.; Gurvich, D.E.; et al. New handbook for standardised measurement of plant functional traits worldwide. *Aust. J. Bot.* **2013**, *61*, 167–234. [CrossRef]
27. Roddy, A.B.; Brodersen, C.R.; Dawson, T.E. Hydraulic conductance and the maintenance of water balance in flowers. *Plant Cell Environ.* **2016**, *39*, 2123–2132. [CrossRef] [PubMed]
28. Zhang, F.-P.; Yang, Y.-J.; Yang, Q.-Y.; Zhang, W.; Brodribb, T.J.; Hao, G.-Y.; Hu, H.; Zhang, S.-B. Floral mass per area and water maintenance traits are correlated with floral longevity in *Paphiopedilum* (Orchidaceae). *Front. Plant Sci.* **2017**, *8*, 501. [CrossRef]

29. Łukowski, A.; Giertych, M.J.; Mąderek, E.; Adamczyk, D.; Karolewski, P. Effect of Scots pine needle age on preference, performance, and overwintering of pine-tree lappet larvae—The distaste for the oldest foliage. *Acta Oecol.* **2022**, *116*, 103836. [CrossRef]
30. Wyka, T.P.; Karolewski, P.; Żytkowiak, R.; Chmielarz, P.; Oleksyn, J. Whole-plant allocation to storage and defense in juveniles of related evergreen and deciduous shrub species. *Tree Physiol.* **2016**, *36*, 536–547. [CrossRef] [PubMed]
31. Zadworny, M.; McCormack, M.L.; Żytkowiak, R.; Karolewski, P.; Mucha, J.; Oleksyn, J. Patterns of structural and defense investments in fine roots of Scots pine (*Pinus sylvestris* L.) across a strong temperature and latitudinal gradient in Europe. *Glob. Chang. Biol.* **2017**, *23*, 1218–1231. [CrossRef]
32. Hansen, J.; Møller, I. Percolation of starch and soluble carbohydrates from plant tissue for quantitative determination with anthrone. *Anal. Biochem.* **1975**, *68*, 87–94. [CrossRef]
33. Haissig, B.E.; Dickson, R.E. Starch measurement in plant tissue using enzymatic hydrolysis. *Physiol. Plant.* **1979**, *47*, 151–157. [CrossRef]
34. Johnson, G.; Schaal, L.A. Accumulation of phenolic substances and ascorbic acid in potato tuber tissue upon injury and their possible role in disease resistance. *Am. Potato J.* **1957**, *34*, 200–209. [CrossRef]
35. Singleton, V.L.; Rossi, J.A. Colorimetry of total phenolics with phosphomolybdic-phosphotungstic acid reagents. *Am. J. Enol. Vitic.* **1965**, *16*, 144–158.
36. Karolewski, P.; Zadworny, M.; Mucha, J.; Napierała-Filipiak, A.; Oleksyn, J. Link between defoliation and light treatments on root vitality of five understory shrubs with different resistance to insect herbivory. *Tree Physiol.* **2010**, *30*, 969–978. [CrossRef]
37. Łukowski, A.; Giertych, M.J.; Adamczyk, D.; Mąderek, E.; Karolewski, P. Preference and performance of the pine-tree lappet *Dendrolimus pini* on various pine species. *Forests* **2021**, *12*, 1261. [CrossRef]
38. Wickham, H.; Francois, R.; Henry, L.; Müller, K. Dplyr: A Grammar of Data Manipulation. 2020. Available online: https://cran.r-project.org/web/packages/dplyr/index.html (accessed on 7 June 2022).
39. Wickham, H.; Chang, W.; Henry, L.; Pedersen, T.L.; Takahashi, K.; Wilke, C.; Woo, K.; Yutani, H. Ggplot2: Create Elegant Data Visualisations Using the Grammar of Graphics. 2020. Available online: https://cran.r-project.org/web/packages/ggplot2/index.html (accessed on 7 June 2022).
40. Revell, L.J. Phytools: Phylogenetic Tools for Comparative Biology (and Other Things). 2020. Available online: https://cran.r-project.org/web/packages/phytools/index.html (accessed on 7 June 2022).
41. Jin, Y.; Qian, H.V. PhyloMaker: An R package that can generate very large phylogenies for vascular plants. *Ecography* **2019**, *42*, 1353–1359. [CrossRef]
42. Blomberg, S.P.; Garland, T.; Ives, A.R. Testing for phylogenetic signal in comparative data: Behavioral traits are more labile. *Evolution* **2003**, *57*, 717–745. [CrossRef]
43. Keck, F. Phylosignal: Exploring the Phylogenetic Signal in Continuous Traits. 2020. Available online: https://cran.r-project.org/web/packages/phylosignal/index.html (accessed on 7 June 2022).
44. Molina-Venegas, R.; Rodríguez, M.A. Revisiting phylogenetic signal; strong or negligible impacts of polytomies and branch length information? *BMC Evol. Biol.* **2017**, *17*, 53. [CrossRef]
45. Chen, C.; Cao, Y.; Chen, H.; Ni, M.; Yu, F. Floral scent compounds and emission patterns of three *Styrax* species. *Dendrobiology* **2021**, *85*, 30–38. [CrossRef]
46. Ortiz, P.L.; Fernández-Díaz, P.; Pareja, D.; Escudero, M.; Arista, M. Do visual traits honestly signal floral rewards at community level? *Funct. Ecol.* **2021**, *35*, 369–383. [CrossRef]
47. Lussu, M.; De Agostini, A.; Cogoni, A.; Marignani, M.; Cortis, P. Does size really matter? A comparative study on floral traits in orchids with two different pollination strategies. *Plant Biol.* **2019**, *21*, 961–966. [CrossRef] [PubMed]
48. Juillet, N.; Scopece, G. Does floral trait variability enhance reproductive success in deceptive orchids? *Perspect. Plant Ecol. Evol. Syst.* **2010**, *12*, 317–322. [CrossRef]
49. Zhang, C.; Li, J.; Willis, C.G.; Ma, Z. Among-population variation in seed mass for 190 Tibetan plant species: Phylogenetic pattern and ecological correlates. *Glob. Ecol. Conserv.* **2020**, *23*, e01163. [CrossRef]
50. Martin, A.R.; Doraisami, M.; Thomas, S.C. Global patterns in wood carbon concentration across the world's trees and forests. *Nat. Geosci.* **2018**, *11*, 915–920. [CrossRef]
51. Castro, S.A.; Silveira, F.A.; Marcato, M.S.; Lemos-Filho, J.P. So close, yet so different: Divergences in resource use may help stabilize coexistence of phylogenetically-related species in a megadiverse grassland. *Flora* **2018**, *238*, 72–78. [CrossRef]
52. Reich, P.B.; Walters, M.B.; Ellsworth, D.S. Leaf age and season influence the relationships between leaf nitrogen, leaf mass per area and photosynthesis in maple and oak trees. *Plant Cell Environ.* **1991**, *14*, 251–259. [CrossRef]
53. Ernst, W.H.O.; Kuiters, A.T.; Nelissen, H.J.M.; Tolsma, D.J. Seasonal variation in phenolics in several savanna tree species in Botswana. *Acta Bot. Neerl.* **1991**, *40*, 63–74. [CrossRef]
54. Kenis, J.D.; Silvente, S.T.; Trippi, V.S. Nitrogen metabolism and senescence-associated changes during growth of carnation flowers. *Physiol. Plant.* **1985**, *65*, 455–459. [CrossRef]
55. McMann, N.; Peichel, A.; Savage, J.A. Early spring flowers rely on xylem hydration but are not limited by stem xylem conductivity. *New Phytol.* **2022**, *233*, 838–850. [CrossRef]
56. Siatka, T.; Kašparová, M. Seasonal variation in total phenolic and flavonoid contents and DPPH scavenging activity of *Bellis perennis* L. flowers. *Molecules* **2010**, *15*, 9450–9461. [CrossRef] [PubMed]

57. Petruzzellis, F.; Palandrani, C.; Savi, T.; Alberti, R.; Nardini, A.; Bacaro, G. Sampling intraspecific variability in leaf functional traits: Practical suggestions to maximize collected information. *Ecol. Evol.* **2017**, *7*, 11236–11245. [CrossRef]
58. Albert, C.H.; Grassein, F.; Schurr, F.M.; Vieilledent, G.; Violle, C. When and how should intraspecific variability be considered in trait-based plant ecology? *Perspect. Plant Ecol. Evol. Syst.* **2011**, *13*, 217–225. [CrossRef]
59. Violle, C.; Enquist, B.J.; McGill, B.J.; Jiang, L.; Albert, C.H.; Hulshof, C.; Jung, V.; Messier, J. The return of the variance: Intraspecific variability in community ecology. *Trends Ecol. Evol.* **2012**, *27*, 244–252. [CrossRef] [PubMed]
60. Violle, C.; Navas, M.-L.; Vile, D.; Kazakou, E.; Fortunel, C.; Hummel, I.; Garnier, E. Let the concept of trait be functional! *Oikos* **2007**, *116*, 882–892. [CrossRef]
61. Datta, R.; Chamusco, K.C.; Chourey, P.S. Starch biosynthesis during pollen maturation is associated with altered patterns of gene expression in maize. *Plant Physiol.* **2002**, *130*, 1645–1656. [CrossRef] [PubMed]
62. Monteiro, J.A.; Nell, T.A.; Barrett, J.E. Effects of exogenous sucrose on carbohydrate levels, flower respiration and longevity of potted miniature rose (*Rosa hybrida*) flowers during postproduction. *Postharvest Biol. Technol.* **2002**, *26*, 221–229. [CrossRef]
63. Ranwala, A.P.; Miller, W.B. Comparison of the dynamics of non-structural carbohydrate pools in cut tulip stems supplied with sucrose or trehalose. *Postharvest Biol. Technol.* **2009**, *52*, 91–96. [CrossRef]
64. Petersen, M. Rosmarinic acid: New aspects. *Phytochem. Rev.* **2013**, *12*, 207–227. [CrossRef]

Publikacja 3.

Paź-Dyderska S., Jagodziński A.M. 2024. Potential of reproductive traits in functional ecology: A quantitative comparison of variability in floral, fruit, and leaf traits. Ecology and Evolution 14, e11690. https://doi.org/10.1002/ece3.11690

Impact Factor 5-letni (2023): 2,9

Punktacja MNiSW (2024): 100

Received: 12 February 2024 | Revised: 10 June 2024 | Accepted: 20 June 2024

DOI: 10.1002/ece3.11690

Ecology and Evolution Open Access WILEY

RESEARCH ARTICLE

Potential of reproductive traits in functional ecology: A quantitative comparison of variability in floral, fruit, and leaf traits

Sonia Paź-Dyderska[1] | **Andrzej M. Jagodziński**[1,2]

[1]Institute of Dendrology, Polish Academy of Sciences, Kórnik, Poland

[2]Poznań University of Life Sciences, Faculty of Forestry and Wood Technology, Department of Game Management and Forest Protection, Poznań, Poland

Correspondence
Sonia Paź-Dyderska, Institute of Dendrology, Polish Academy of Sciences, Parkowa 5, 62-035 Kórnik, Poland.
Email: sdyderska@man.poznan.pl

Funding information
Narodowe Centrum Nauki, Grant/Award Number: 2020/37/N/NZ8/00387; Institute of Dendrology of the Polish Academy of Sciences

Abstract

Despite their claimed low intraspecific variability, plant reproductive traits are less frequently used in functional ecology. Here we focused on underrepresented plant organs, i.e. flowers and fruits, by comparing their traits with well-established leaf traits. We evaluated 16 functional traits (six floral, six fruit, and four leaf traits) in a randomly selected group of woody species under comparable environmental conditions. We aimed to assess interspecific and intraspecimen variability and explore the potential of the proposed flower and fruit traits for ecological research. Traits related to the dry mass of flowers and fruits exhibited the highest interspecific variability, while carbon content traits in flowers and leaves had the lowest. At a specimen level, specific leaf area revealed the highest variation. Carbon content traits for all organs demonstrated the least intraspecimen variability, with flower carbon content being the least variable. Our study revealed connections between the newly proposed traits and widely recognized functional traits, uncovering intriguing links between the established traits and the floral and fruit traits upon which we focused. This complements the already well-recognized variability in plant form and function with additional insights into reproductive processes.

KEYWORDS
floral and fruit traits, organs, plant functional traits, reproduction, traits variability, trees and shrubs

TAXONOMY CLASSIFICATION
Biodiversity ecology, Botany, Chemical ecology, Community ecology, Ecosystem ecology, Functional ecology, Life history ecology

1 | INTRODUCTION

Enhancing the predictive processes for future environmental changes is essential within the context of global climatic changes (Intergovernmental Panel on Climate Change, 2023). Improving these forecasts can be achieved through a more extensive and frequent integration of plant functional traits into ecological research (Liu et al., 2021). Plant functional traits encompass morphological, phenological, and physiological characteristics that define the growth, reproduction, and survival of plants, spanning from individual specimens, through populations and species, to entire plant communities (Díaz & Cabido, 2001; Lavorel & Garnier, 2002; Violle et al., 2007). The broad concept of functional traits offers significant utility for ecological studies, including the ability to predict ecosystem functioning and its responses to changing climates (Kühn et al., 2021; Liu et al., 2021), better understand species adaptations (Bussotti et al., 2015), assess biodiversity beyond species composition alone (Petchey & Gaston, 2006), inform conservation and restoration efforts (Ostertag et al., 2015), and assess resilience to disturbances and biological invasions (te Beest et al., 2015). Additionally, functional traits are valuable for the existing intercorrelations between them. Knowledge of the value of one trait often enables the assessment of another, even if measuring the latter involves greater difficulty, time, or effort (Díaz et al., 2016; Milla & Reich, 2007). Still, when considering trade-offs between traits, it is essential to recognize that they result from different resource acquisition and allocation patterns, which are shaped by both community context and resource availability (Agrawal, 2020). Also, a holistic functional approach involving the traits of different plant organs can serve as a useful, quantified reflection of plant life strategies (Adler et al., 2014; Chai et al., 2016; Laughlin et al., 2010). Currently, many of the functional traits are used as tools for objective comparisons of different life strategies (Adler et al., 2014; Kattenborn et al., 2017) but also for predicting future changes in plant communities (Metcalfe et al., 2020; van Bodegom et al., 2014) or in their assembly (Laughlin, 2014; Laughlin et al., 2012).

Despite the numerous benefits derived from functional traits in ecological research, there are significant drawbacks related to the completeness and availability of functional data (Cordlandwehr et al., 2013; Johnson et al., 2021). The phylogenetic and geographic coverage of data about particular species is biased, predominantly favoring economically important woody species and regions in the Global North (Cornwell et al., 2019; Kattge et al., 2020). Additionally, even when a species is present in a database, it is often inadequately represented by a limited number of measurements, neglecting intraspecific variability (Siefert et al., 2015).

While functional research has extensively covered certain plant organs, such as leaves, stems, and seeds, there has been an uneven recognition of different plant organs (Paź-Dyderska & Jagodziński, 2023). The leaf economic spectrum has guided further studies (Wright et al., 2004), preceded by the leaf-height-seed (LHS) concept by Westoby (1998). The study conducted by Díaz et al. (2016) effectively explained the variability of plant form and function at a global scale. However, recent studies emphasize the necessity for a deeper understanding of plant life strategies, urging a broader consideration of organs (Bardgett et al., 2014; Kleyer & Minden, 2015; Roddy et al., 2021), especially roots, which has prompted the dynamic development of this field of ecology, including the establishment of standardized protocols for root data collection and extensive root trait databases (Guerrero-Ramírez et al., 2021; Iversen et al., 2017). Despite this progress, the coverage of organs through measurements remains uneven, with flowers and fruits being underrepresented and lacking standardized data collection protocols. So far, there have been limited papers on this topic, both for flowers (Bosch et al., 1997; Cresswell, 1998; Svensson, 1992) and fruits (Birkhold et al., 1992; Kourmpetli & Drea, 2014; Levey et al., 2000). Even fewer studies discuss flower physiology, anatomy, and morphology. Some of the questions still needing answers include potential threats to plant reproduction under changing climate conditions (Aun et al., 2024), the constraining role of water availability for flower maintenance (Lambrecht, 2013), and the vulnerability of flowers to xylem damage due to drought (Zhang & Brodribb, 2017). Major gaps in our knowledge of flowers and fruits may result from the lack of standardized data collection protocols, low species coverage, and unbalanced geographic and phylogenetic representation in data from different regions (E-Vojtkó et al., 2020, 2022).

Recent years, however, have witnessed a positive shift, marked by an increasing number of studies focusing on floral (Chartier et al., 2017; Roddy, 2019; Roddy et al., 2021) and fruit traits (Acevedo-Quintero et al., 2023; de Paz et al., 2018; Garrido et al., 2023). This trend is understandable, given that the diverse forms of flowers and fruits offer a wide range of valuable information. So far, several works discuss flower traits, which could significantly contribute to our understanding of plant biology and ecology. For example, flower traits such as reflectance, scent, and morphology can profoundly impact interactions with pollinators and herbivores (Junker & Parachnowitsch, 2015). Similarly, fruit traits can significantly affect ecological interactions. Factors such as size, color, and odor can influence interactions with dispersers, strongly impacting seed dispersal and colonization possibilities (Mahandran et al., 2023; Rodríguez et al., 2013). Furthermore, variation in floral and fruit traits can contribute to plant lineage diversification over evolutionary time as plants adapt to different ecological niches and selective pressures (Bolmgren & Eriksson, 2005; Gómez et al., 2016; Van der Niet et al., 2014). Additionally, floral and fruit traits reflect investments in resources by plants. Floral traits represent investments by plants to attract pollinators and ensure successful reproduction (Ashman & Schoen, 1996; Teixido et al., 2016). Similarly, fruit production represents a significant investment of resources to ensure successful seed dispersal and colonization, with plants allocating resources to produce fruits with various traits, balancing the costs and benefits based on environmental conditions and ecological contexts (Anderson & Hill, 2002). Therefore, floral and fruit functional traits represent the diverse array of plant reproductive strategies. These traits are often deemed highly stable within species (Cresswell, 1998), suggesting that their low intraspecific variability could mitigate methodological drawbacks associated with using mean trait values from databases. Also, flower and fruit traits are critical determinants of plant fitness by influencing pollination success, herbivore deterrence, seed dispersal, and resource allocation (Gavini et al., 2018; Stournaras & Schaefer, 2017). In this context, the functional traits of flowers and fruits possess significant yet underrated potential in functional research. However, their usability would require quantified verification, especially regarding the aspect of their variability.

To date, comparable studies have predominantly concentrated on assessing the traits of individual organs, quantifying the variability within a specific organ (Paź-Dyderska & Jagodziński, 2024; Poorter et al., 2009; Snell et al., 2019). This prompted our exploration into the traits of three distinct organs, aiming to conduct a comparative analysis. In this current study, we chose to investigate the traits of underrepresented organs, namely, flowers and fruits, and compare them with the well-established traits of leaves. Given that this represents one of the initial endeavors of its kind, we opted to exclusively focus on woody plants. This deliberate limitation aims to constrain potential sources of variability within the species pool. To minimize potential variability arising from environmental conditions, we chose to conduct the study in an Arboretum, where specimens grow in conditions similar to common garden settings, thus justifying the comparisons of trait measurements (Fanal et al., 2021; Faraji & Karimi, 2022; Perez et al., 2019).

We aimed to evaluate the variability of 16 functional traits (comprising six floral, six fruit, and four leaf traits) among a randomly selected group of woody species growing in comparable environmental conditions. Our focus was on assessing both interspecific and intraspecimen levels of variability (Liu et al., 2021; Westerband et al., 2021). Incorporating the intraspecific level of variation proved challenging in this study design. The Arboretum, despite its extensive collection, frequently lacks numerous specimens of the same species, with singular specimens being more common. Subsequently, we decided to check whether there are relationships among the interspecific variability of the traits studied, and their intracanopy variability represented by the plasticity index value. Lastly, we aimed to evaluate the potential of the proposed fruit and flower traits for future ecological research.

We hypothesized that (1) there would be a higher level of variation in floral and fruit traits at the interspecific level, given the generally more diversified forms of flowers and fruits compared to leaves among the subset of species studied here. Second, we hypothesized (2) an opposite pattern at the intraspecimen level, with fruits and flowers showing lower intraspecimen variability compared to leaves. This is because they are more evolutionarily predisposed to stability in form (Cresswell, 1998; van Kleunen et al., 2008), unlike leaves, which, as resource-acquisition organs, exhibit higher plasticity and adaptability to changing light availability (Paź-Dyderska et al., 2020; Poorter et al., 2009). Finally, we hypothesized that (3) floral and fruit traits would contribute new information to the global spectrum of plant form and function (Díaz et al., 2016; E-Vojtkó et al., 2022), suggesting their potential usability in future ecological research.

2 | METHODS

2.1 | Study area

Our study was conducted within the Kórnik Arboretum in western Poland (52.2448° N, 17.0969° E, 75 m a.s.l.). Renowned as one of Poland's oldest and most extensive collections, it houses ca. 3500 taxa of woody plants, including numerous ornamental cultivars. Examining plant traits, especially in trees with extended maturation periods, requires consideration of plant age. The Arboretum's comprehensive dendrological collection renders it an appealing setting for such investigations. We have previously highlighted the advantages of utilizing the Arboretum for studies on the variability of specific leaf area (Paź-Dyderska et al., 2020), floral chemical and size-related traits (Paź-Dyderska et al., 2022; Paź-Dyderska & Jagodziński, 2024), and seed mass (Dylewski et al., 2024).

Historically, the Arboretum's management prioritized cognitive and ornamental purposes and was not explicitly designed for ecological studies. While some specimens were densely planted, others were isolated or arranged in small groups, forming alleys, potentially leading to uneven light distribution among individuals. Nonetheless, despite these considerations, the Arboretum stands out as one of the optimal choices for studying trait variability across a diverse range of species (Dosmann & Groover, 2012; Edwards et al., 2018; Fanal et al., 2021).

The study site is characterized by a temperate climate, featuring an average growing season lasting 220 days, a mean annual precipitation of 544 mm, and a mean annual temperature of 8.3°C. These climate parameters, documented in the Arboretum between 1948 and 2005 (Cedro & Iszkuło, 2011), set the backdrop for our research. In 2021 and 2022, during our data collection period, we gathered information from the meteorological station in the Arboretum, indicating mean annual precipitation and mean annual temperatures of 407 and 486 mm, and 9.9 and 10.1°C, respectively. The Arboretum offers consistent environmental conditions, encompassing both climate and soil type, providing an ideal setting for comparing traits across a diverse range of systematic and functional groups. This uniformity minimizes the influence of climate variations and extreme conditions, such as droughts, floods, or other disturbances, on the variability of the studied traits. Consequently, we assumed that comparing specimens growing in the Arboretum is justified, as the conditions in the Arboretum closely resemble a common garden design.

2.2 | Data collection

We randomly selected a representative sample comprising 79 woody plant species cultivated under controlled common garden conditions (Figure S1), as outlined in our previous work (Paź-Dyderska et al., 2020, 2022). Our data collection spanned from March 2021 to August 2022, emphasizing the examination of fully developed flowers, leaves, and fruits free from any damage caused by fungi, herbivores, or abiotic factors like hail or drought. Although collection protocols for floral or fruit traits are not yet widespread, we decided to incorporate established ideas from studies previously conducted in botanical gardens (Roddy, 2019; Roddy et al., 2016; Zhang et al., 2017). This methodology had been successfully employed in our previous investigation of floral traits within the Arboretum (Paź-Dyderska et al., 2022; Paź-Dyderska & Jagodziński, 2024). For leaves, we employed an approach adapted from Pérez-Harguindeguy et al. (2013).

All organs were harvested at the zenith of their development phase, ensuring their complete maturation while preserving optimal conditions. To assess intra-canopy trait variability, we gathered samples from two light regimes within each specimen, specifically targeting the shadiest and sunniest sections of the crown. This resulted in six samples for each specimen: two floral, two fruit, and two leaf samples. One sample from each pair originated from the sunny part, while the other came from the shady part of the specimen.

Consistent with our previous study in the Arboretum, we selected organs for the investigation based on qualitative observations, refraining from measuring light availability (Paź-Dyderska et al., 2020, 2022). The collection process involved the use of a 6 m long pole pruner. To mitigate the influence of tree location on our results, we harvested samples exposed to sunlight from the southern sides of the crowns and shaded samples from the northern sides, resulting in the collection of two samples per specimen. Each sample typically consisted of 10 flowers, fruits, and leaves, respectively, resulting in a total of 20 flowers, fruits, and leaves per specimen. However, exceptions were made for species with exceptionally large flowers, such as *Magnolia tripetala*, where a smaller sample size was chosen to avoid potential harm to the valuable specimen. Adjustments were also made for species that did not produce a large number of fruits. Some species did not produce fruits, potentially influenced by year-to-year variability in environmental conditions such as late-spring frost or summer drought. Additionally, the absence of a sufficient number of male specimens capable of fertilization could contribute to the lack of fruit production in some dioecious species. Furthermore, herbivory, particularly on fleshy fruits, was frequent, leading to many fruits being consumed by birds before reaching full ripening. As a result, samples of flowers and leaves were collected for 79 species, while fruits were obtained from 33 species, resulting in a total of 382 samples. This number is derived from the collection of double samples from each specimen, that is, samples from both light variants.

In terms of flower collection, for dioecious species, our exclusive focus was on female flowers since they transform into fruits, which are also the primary focus of our study. This rationale justified a comprehensive comparison of their traits. Throughout the sampling process, we systematically collected data on both the pedicel and peduncle, and for leaves, we included information on the petiole. After collection, we placed the samples in ziplock bags. This was done to minimize the risk of damage to the delicate samples and prevent moisture loss, which could potentially impact size-related measurements. Subsequently, we stored the samples in a refrigerator to decelerate wilting, allowing them to await further trait measurements under optimal conditions.

2.3 | Traits measurements

We examined a total of 16 traits for each sampled species, categorizing them into six floral, six fruit, and four leaf traits (Table 1). The floral traits comprised flower length (mm), width (mm), carbon content (%), nitrogen content (%), C:N ratio, and dry biomass (g). Similarly, fruit traits included fruit length (mm), diameter (mm), carbon content (%), nitrogen content (%), C:N ratio, and dry biomass (g). Leaf traits included specific leaf area (SLA, $cm^2\ g^{-1}$), carbon content (%), nitrogen content (%), and C:N ratio. In our interspecific analyses, we calculated the mean values for each trait. For intracanopy analyses, we computed mean values from two samples collected from each specimen, specifically, from both the sunny and shaded parts of the specimen.

We measured flower length, width, fruit length, and diameter using electronic calipers (with an accuracy of 0.001 mm) within 24 h of sample collection. Mean values were then calculated for each sample. Subsequently, we dried all flowers and fruits in an oven with forced air circulation at 65°C (ULE 600 and UF450, Memmert GmbH + Co. KG, Regensburg, Germany) until reaching a constant mass. We determined dry biomass using scales with an accuracy of 0.001 g.

We employed WinFOLIA 2020 PRO software (Regent Instruments Inc., Quebec, Canada) to scan leaves (along with the petiole) from each sample within 24 h of collection, measuring their area at a resolution of 300 DPI. Subsequently, we dried the leaves in an oven with forced air circulation at 65°C (ULE 600 and UF450, Memmert GmbH + Co. KG, Germany) until a constant mass was achieved. Following the drying process, we weighed the leaf samples using scales with an accuracy of 0.001 g. SLA, calculated as the ratio of leaf area to leaf dry biomass, was derived from these measurements.

Lastly, we assessed carbon and nitrogen content among the samples using an ECS CHNS – O 4010 Elemental Combustion System (Costech Instruments, Italy/USA) and a CHNS/O Analyser 2400 Series II (Perkin Elmer, USA).

2.4 | Data analysis

For data analysis, we used the R software (R Core Team, 2023). All mean values were followed by standard errors (SE). For data processing, we used the dplyr package, and ggplot2 for visualization (Wickham, Chang, et al., 2020; Wickham, Francois, et al., 2020). To compare the variability of the studied traits at the interspecific level, we evaluated differences in trait coefficients of variation (CV, calculated as standard deviation divided by mean) between two traits using Krishnamoorthy and Lee's (2014) modified signed-likelihood ratio test (M-SLR test). This test was implemented through the cvequality::mslr_test() function (Marwick & Krishnamoorthy, 2019). We decided to use the M-SLR test due to lower type I error rates and increased power across a range of conditions compared to the widely used asymptotic test of Feltz and Miller (1996), as noted by Funk (2008) and Paquette et al. (2012). Additionally, the M-SLR test accommodates uneven sample numbers, a crucial feature for our study design. To avoid an increased risk of type I errors when performing multiple hypotheses tests (pairs of CVs for each trait), we also applied Holm-Bonferroni corrections (Holm, 1979). Analyses involving interspecific variability were based on averaged trait values from both sun and shade parts of the crowns.

TABLE 1 Overview of studied traits and their biological significance.

Trait	Type of trait	Biological significance
Specific leaf area ($cm^2 g^{-1}$)	Morphological	Higher SLA values indicate thinner leaves with larger surface areas, enhancing photosynthetic efficiency and resource acquisition. SLA also reflects trade-offs between growth rates and resource conservation. SLA influences plant defense mechanisms, environmental adaptation, and ecosystem functioning, shaping ecosystem processes such as carbon and nutrient cycling (Reich, 2014; Wright et al., 2004)
Leaf C (%)	Physiological	Leaf carbon content fuels the synthesis of essential organic compounds, supporting plant growth and development (Reich, 2014; Wright et al., 2004)
Leaf N (%)	Physiological	Higher leaf nitrogen content enhances photosynthetic rates and growth, contributing to increased productivity and plant resilience. It is also necessary for protein synthesis and enzyme activity. Leaf nitrogen content drives plant-herbivore interactions and nutrient turnover rates (Díaz et al., 2016; Reich et al., 1998; Wright et al., 2004)
Leaf C:N (dimensionless)	Physiological	Optimal C:N ratios maintain nutrient balance, supporting vital processes like growth and reproduction. Deviations from this balance can signal nutrient limitations, impacting plant productivity. Additionally, C:N ratios influence plant quality as food for herbivores and decomposers, shaping nutrient cycling rates (Reich, 2014; Wright et al., 2004)
Flower C:N (dimensionless)	Physiological	This ratio reflects the allocation of carbon and nitrogen resources during flower development, influencing reproductive investment strategies and flower quality. Additionally, flower C:N ratios may influence flower defense mechanisms against herbivores and pathogens (Farré-Armengol et al., 2013; Santiago & Sharkey, 2019)
Flower length (mm)	Morphological	Flower length influences the attraction of specific pollinators by accommodating their mouthparts and facilitating access to floral rewards. This trait promotes reproductive efficiency by enhancing pollen transfer between flowers and supporting cross-pollination. Variation in flower length reflects coevolutionary dynamics with pollinators (E-Vojtkó et al., 2022; Gómez et al., 2016)
Flower width (mm)	Morphological	Flower width influences the type of pollinators attracted to the flower, with wider flowers often accommodating bees, butterflies, and other pollinators seeking ample landing space and access to nectar and pollen. This trait impacts reproductive success by enhancing pollination efficiency and seed production (E-Vojtkó et al., 2022; Gómez et al., 2016)
Flower dry biomass (g)	Morphological, physiological	Flower dry biomass reflects the resources allocated to flower production, with higher dry biomass indicating greater reproductive investment by the plant. Larger, more attractive flowers with higher dry biomass might attract more pollinators and achieve successful pollination, and seed set (Lussu et al., 2019; Teixido et al., 2016)
Flower C (%)	Physiological	Carbon serves as a structural component in flower tissues, contributing to their strength and durability. Flower carbon content also influences pollinator attraction and reward quality, as well as plant-herbivore interactions, by affecting floral palatability and defense mechanisms (Heberling et al., 2019)
Flower N (%)	Physiological	Nitrogen is essential for flower development, determining pollen production. Flower nitrogen content affects pollinator attraction and reward quality. After pollination, nitrogen-rich floral tissues contribute to soil nutrient pools through decomposition, supporting ecosystem productivity (Ma et al., 1997; Pers-Kamczyc et al., 2020; Santiago & Sharkey, 2019)
Fruit length (mm)	Morphological	Fruit length influences seed dispersal mechanisms and survival. It mediates interactions between plants and frugivores, shaping seed dispersal patterns (Bentos et al., 2014; Stournaras & Schaefer, 2017)
Fruit diameter (mm)	Morphological	Fruit diameter impacts seed dispersal efficiency by influencing dispersal mechanisms and the preferences of frugivores, reflecting plant reproductive strategies (Bentos et al., 2014; Kourmpetli & Drea, 2014)
Fruit dry biomass (g)	Morphological, physiological	It reflects the investment of resources into fruit development, influencing reproductive success, and seed dispersal mechanisms. Additionally, fruit dry biomass contributes to the nutritional value of fruits for seed dispersers and consumers (Bentos et al., 2014; Kourmpetli & Drea, 2014)
Fruit C (%)	Physiological	Carbon-rich fruits contribute to the structural integrity of the fruit, enhancing seed germination and seedling establishment. It also forms defensive compounds, such as phenols and tannins. That way, fruit carbon content influences interactions between plants and seed dispersers. It also contributes to nutrient cycling and soil fertility when fruits decompose (Feng et al., 2014; Rodríguez et al., 2013)
Fruit N (%)	Physiological	Nitrogen-rich fruits provide essential nutrients for consumers, attracting a diverse range of frugivores and facilitating seed dispersal. After fruit consumption, the remaining nitrogen supports soil fertility and ecosystem productivity through decomposition (de Paz et al., 2018; Levey et al., 2000)
Fruit C:N (dimensionless)	Physiological	This ratio reflects the allocation of carbon and nitrogen resources during fruit development. It also affects seed dispersal strategies by shaping fruit attractiveness to seed dispersers (Birkhold et al., 1992; Garrido et al., 2023)

Note: Type of trait according to Violle et al. (2007).

To compare the level of intraspecimen trait variability we used the plasticity index (PI). PI was calculated by evaluating the difference between maximum and minimum trait values, dividing it by the maximum trait values, following the methodology proposed by Valladares et al. (2000). In our study, the maximum and minimum values were obtained from the mean trait values in the two samples, each collected under sun and shade conditions. Consequently, the higher of the two values represented our maximum, and the lower represented our minimum. Analyses involving intracanopy trait variability comprised two samples (one from each light variant, i.e., sun or shade). We used PI for each species as a standardized measure of effect sizes, independent of trait values. For evaluating the impact of light variants on trait values, we employed a phylogenetic paired t-test using the phyl.pairedttest function from the phytools package (Revell, 2020). In this *t*-test we compared PI of each pair of traits, using species as data points. This test expands on the traditional paired *t*-test by taking into account the phylogenetic similarity of observations. We acquired information about species phylogenetic similarity using a phylogenetic tree obtained from the V.PhyloMaker2 package (Jin & Qian, 2022). Similar to the interspecific analyses, here we also applied the Holm–Bonferroni correction (Holm, 1979).

Given our aim to compare the traits introduced in this study with the established traits constituting the global spectrum of plant form and function, we found it necessary to obtain data for the three traits not measured by us in the study (i.e., height, seed mass, and specific stem density) from the TRY database (Kattge et al., 2020). Since the TRY database did not provide values for these traits for all the studied species, we employed a data imputation approach to fill in the gaps. This method involved relying on correlations among traits and between traits and phylogeny, following a methodology used in our previous study (Paź-Dyderska & Jagodziński, 2023) and consistent with the approach outlined by Pyšek et al. (2015). For imputation, we used known values of traits and phylogenetic eigenvectors, derived from the phylogenetic tree using the PVR package (Santos, 2018). These variables were used in trait-wise random forest based imputations implemented in the missForest package (Stekhoven & Bühlmann, 2012). We decided to reinforce predictive power by phylogenetic eigenvectors as Penone et al. (2014) revealed that it can significantly increase accuracy of estimating missing trait values. By adopting this approach, we ensured a comprehensive dataset for analysis, thereby maintaining the integrity of our study despite the absence of values for some traits. We imputed missing flower traits data for seven species (8.8%), fruit traits for 46 species (58.2%), height for 15 species (19.0%), seed mass for 21 species (26.6%), and SSD for 49 species (62.0%). Normalized RMSE of imputation was 0.50. Such a proportion of missing data still allows for robust data analyses (Stewart et al., 2023).

To examine potential relationships among the newly proposed floral and fruit traits and well-established traits within the global spectrum of plant form and function (Díaz et al., 2016), we performed Principal Component Analysis (PCA) using the vegan package (Oksanen et al., 2022). Using PCA allowed us to explore connections between various traits and evaluate whether the new traits represent additional dimensions of plant form and function variability among the studied species. Prior to PCA we standardized trait values by centering (i.e., mean subtraction) and scaling (i.e., dividing by standard deviation). We assessed bivariate relationships for each pair of studied traits following the method proposed by Zheng et al. (2009), using the corphylo function from the ape package (Paradis & Schliep, 2019).

3 | RESULTS

3.1 | Interspecific variability

We observed that among the studied traits, those related to the dry mass of flowers and fruits had the highest interspecific variability, while traits associated with the carbon content in flowers and leaves had the lowest variability (Table 2, Figure 1). Specifically, flower dry biomass stood out with a CV = 4.351, showcasing the highest interspecific variability among the 16 analyzed traits. This was followed by fruit dry biomass (CV = 2.510) and fruit nitrogen content (CV = 2.419). Conversely, the least variable traits were those related to carbon. Size-related traits, such as flower length and width, and fruit length and diameter, represented an intermediate level of variation. SLA demonstrated a limited level of interspecific variation (CV = 0.369), ranking below the variability of traits related to flower and fruit dry mass, as well as size-related traits of flowers (CV of flower length = 1.172 and flower width = 0.974) and fruits (CV of fruit length = 0.844 and of diameter = 0.767).

3.2 | Intraspecimen variability

Among the studied traits, SLA exhibited the highest variation within a specimen, with a mean PI of 29.963% (Table 3, Figure 2). This was followed by the dry biomass of flowers (PI = 17.541%) and fruits (PI = 15.158). In parallel to interspecific analyses, carbon-content traits for all organs demonstrated the least variability, with flower carbon content being the least variable (PI = 1.347%). Nitrogen-related traits represented intermediate levels of intracanopy variability (PI values for flowers, fruits, and leaves were 11.261%, 12.564%, and 11.139%, respectively). Similarly, size-related traits showed values of 9.226% for flower length, 10.317% for flower width, 6.353% for fruit length, and 5.884% for fruit diameter.

3.3 | Interspecific versus intraspecimen variability of the traits studied

In the visualized comparison of mean interspecific and intracanopy variability (Figure 3), we identified variations not only in the mean values of variability but also in their ranges. The traits reflecting carbon content in all three analyzed organs demonstrated the least

TABLE 2 Species-level averaged trait values.

Variable	Min	Q1	Median	Mean	SE	CV	Q3	Max
Specific leaf area ($cm^2 g^{-1}$)	34.100	171.636	206.255	215.486	8.949	0.369	249.043	565.605
Leaf C (%)	39.580	43.813	44.995	44.747	0.184	0.037	45.723	48.810
Leaf N (%)	1.115	1.890	2.245	2.221	0.063	0.254	2.513	4.405
Leaf C:N (dimensionless)	12.027	20.951	23.270	25.111	0.730	0.258	27.593	48.692
Flower C (%)	40.910	43.630	44.583	44.421	0.162	0.031	45.254	47.405
Flower N (%)	1.295	2.266	2.845	2.966	0.109	0.312	3.370	5.220
Flower C:N (dimensionless)	9.809	15.454	18.512	19.426	0.742	0.324	23.103	40.576
Flower length (mm)	0.681	8.196	14.026	20.655	2.723	1.172	21.048	155.679
Flower width (mm)	0.609	8.941	14.942	20.194	2.214	0.974	23.508	122.605
Flower dry biomass (g)	0.0001	0.005	0.037	0.241	0.118	4.351	0.116	9.166
Fruit length (mm)	3.710	9.964	15.918	24.341	3.577	0.844	36.833	89.419
Fruit diameter (mm)	2.869	7.392	9.257	13.509	1.803	0.767	14.320	45.710
Fruit dry biomass (g)	0.006	0.055	0.162	0.974	0.426	2.510	0.419	12.479
Fruit C (%)	0.553	45.840	47.035	41.986	2.726	0.373	48.535	53.065
Fruit N (%)	0.305	0.800	1.365	10.714	4.511	2.419	1.820	86.827
Fruit C:N (dimensionless)	16.954	38.776	46.245	57.495	6.538	0.653	72.341	232.402

Abbreviations: CV, coefficient of variation; Max, maximum; Min, minimum; Q1, first quartile; Q3, third quartile; SE, standard error.

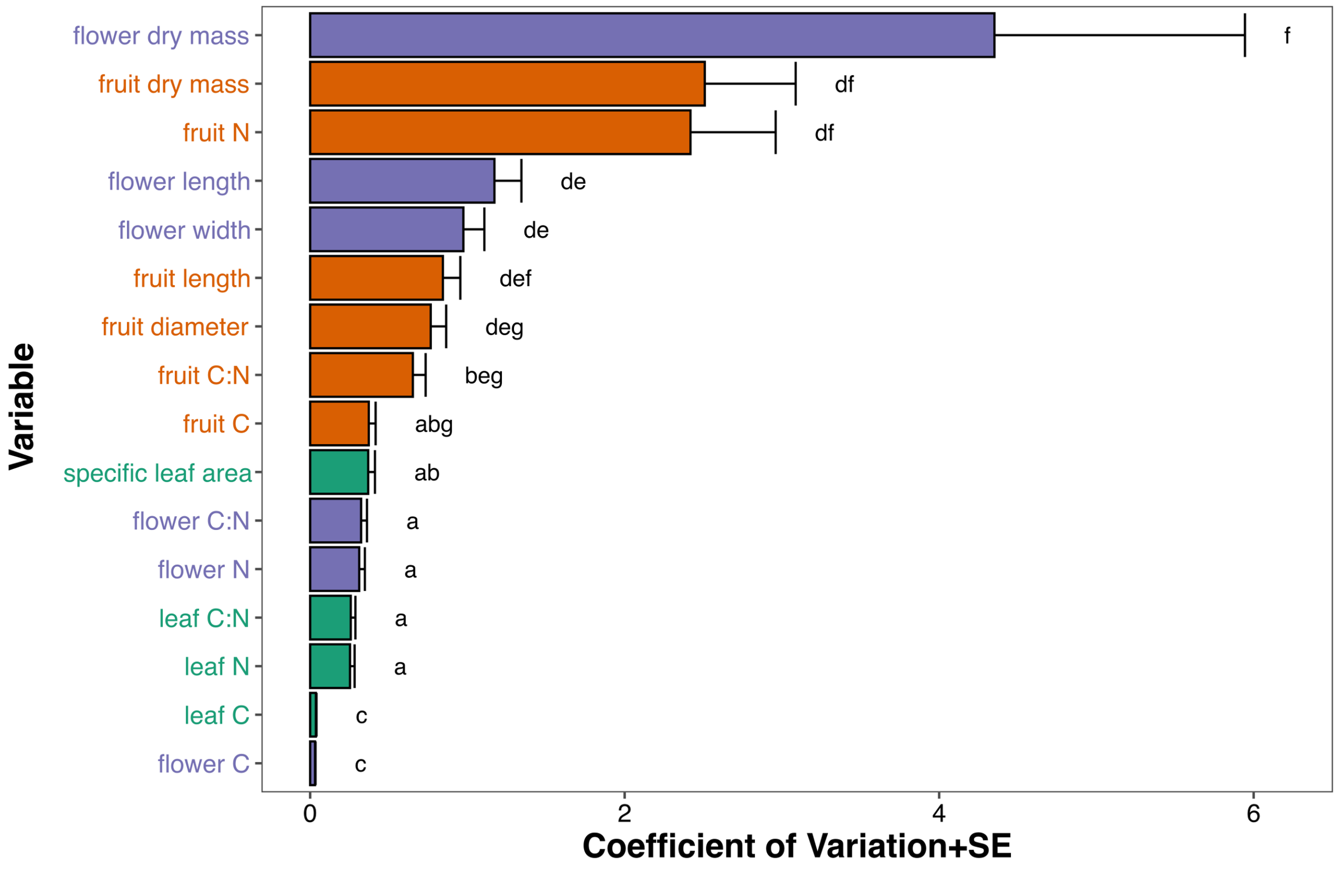


FIGURE 1 Mean + SE coefficient of variation (%) for the functional traits studied. Purple bars represent floral traits, orange bars – fruit traits, and green bars – leaf traits. Traits denoted with the same letter did not differ at *p* = .05 according to M-SLR tests, after application of Holm's correction. For test statistics, see Table S1.

TABLE 3 Plasticity index values (%).

Variable	Min	Q1	Median	Mean	SE	CV	Q3	Max
Specific leaf area ($cm^2 g^{-1}$)	1.054	17.294	30.792	29.963	1.859	0.551	41.103	69.340
Leaf C (%)	0.044	1.097	2.218	2.620	0.227	0.771	3.446	8.619
Leaf N (%)	0.000	5.239	8.955	11.139	0.939	0.749	14.329	38.760
Leaf C:N (dimensionless)	0.254	4.382	9.589	11.082	0.963	0.773	14.266	40.383
Flower C (%)	0.022	0.647	1.173	1.347	0.114	0.720	1.939	4.295
Flower N (%)	0.303	3.730	8.868	11.261	1.251	0.943	14.871	56.959
Flower C:N (dimensionless)	0.096	3.840	8.956	11.228	1.233	0.932	14.668	56.514
Flower length (mm)	0.189	3.050	5.851	9.226	1.295	1.248	9.949	72.728
Flower width (mm)	0.212	3.039	7.283	10.317	1.234	1.063	14.184	68.670
Flower dry biomass (g)	0.000	6.266	12.500	17.541	1.941	0.984	23.479	90.086
Fruit length (mm)	0.264	2.120	6.458	6.353	0.884	0.800	9.498	23.551
Fruit diameter (mm)	0.165	2.627	4.477	5.884	0.795	0.776	7.502	16.776
Fruit dry biomass (g)	0.971	6.742	13.606	15.158	1.682	0.638	24.379	35.103
Fruit C (%)	0.040	0.992	1.998	3.400	0.905	1.529	3.340	24.379
Fruit N (%)	0.000	1.408	9.333	12.564	2.617	1.197	16.770	64.444
Fruit C:N (dimensionless)	0.174	2.535	7.593	12.801	2.612	1.172	15.146	65.377

Abbreviations: CV, coefficient of variation; Max, maximum; Min, minimum; Q1, first quartile; Q3, third quartile; SE, standard error.

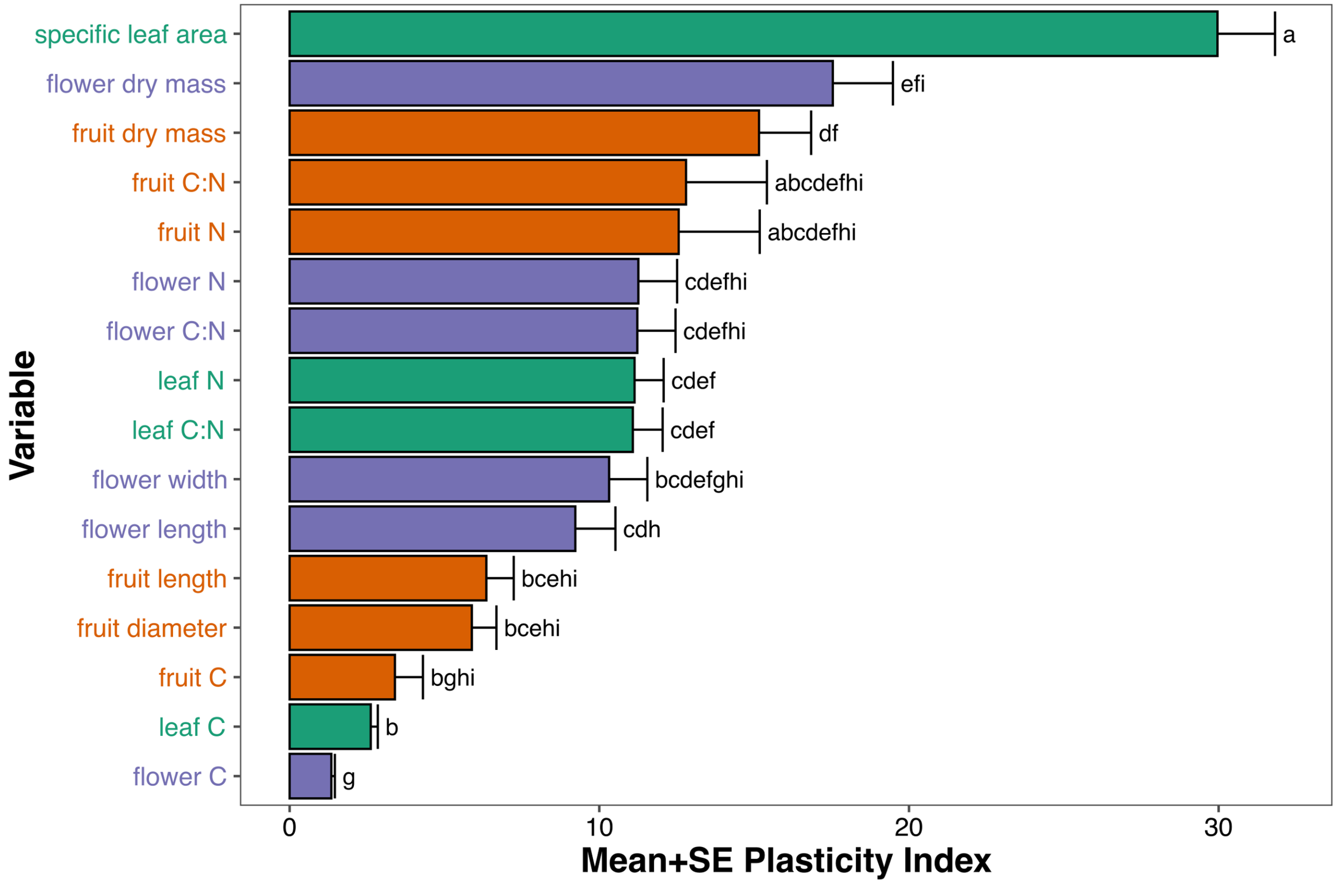


FIGURE 2 Mean + SE plasticity index (%) for the functional traits studied. Purple bars represent floral traits, orange bars – fruit traits, and green bars – leaf traits. Traits denoted with the same letter did not differ at $p = .05$, according to phylogenetic paired t-test, after application of Holm's correction. For test statistics see Table S2.

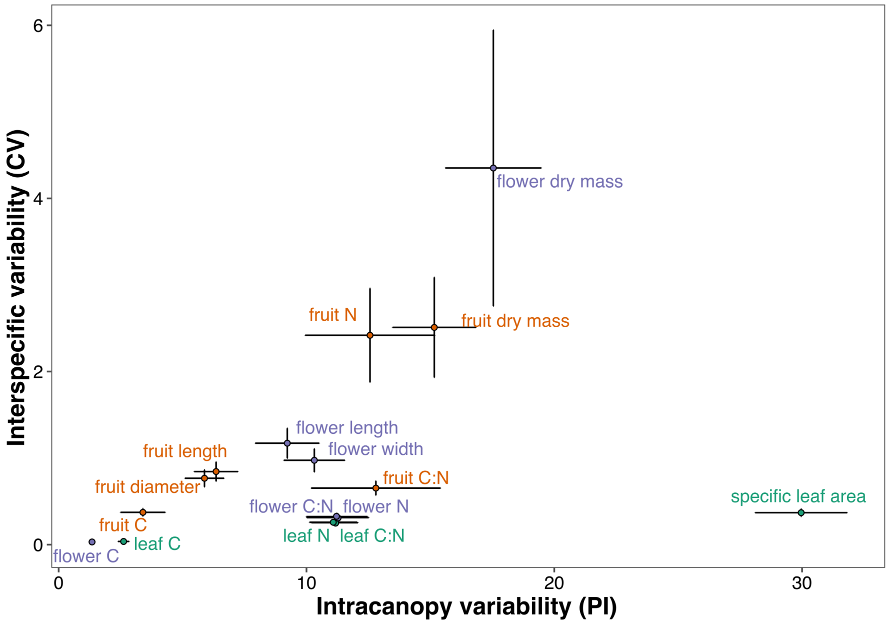


FIGURE 3 Comparison of mean ± SE interspecific trait variability, represented by the coefficient of variability (%) with the intracanopy variability of the respective traits, represented by the plasticity index (%) of a given trait. Purple labels represent floral traits, orange labels – fruit traits, and green labels – leaf traits.

variability, both in terms of interspecific and intracanopy variability. Traits related to size and nitrogen content across all organs exhibited intermediate values of coefficient of variation (CV) and plasticity index (PI). Flower dry mass stood out with the highest range of values representing interspecific variability and a limited range of values representing intracanopy variability. Notably, the position of SLA on the diagram showed particularly high mean intracanopy variability values, along with a wide range, while simultaneously exhibiting a low range of interspecific variability.

3.4 | Relationships between established and novel traits proposed in this study

The PCA revealed the main directions of variation (Figure 4), with the PC1 axis explaining 21.54% of the variability and the PC2 axis explaining 15.22% of the variability. Negative values on the PC1 axis were associated with higher values of three traits proposed by Díaz et al. (2016), namely leaf area, height, and seed mass, along with higher values of mass- and size-related traits of flowers and fruits. Conversely, positive values on the PC1 axis were correlated with specific seed density, which increased proportionally with the values on the PC1 axis. Increasing values on the PC2 axis were correlated with higher nitrogen concentration in all three analyzed organs, as well as increasing SLA. Conversely, the PC2 axis showed a negative correlation with carbon concentration and C:N ratio, regardless of the organ analyzed. None of traits measured by us revealed a separate dimension of variability in trait space. Analysis of bivariate correlations revealed the strongest relationships among traits expressing organ sizes (e.g., fruit length and diameter), as well as C:N ratios and N contents (Figure 5). Seed mass was positively correlated with fruit dimensions and dry mass and height.

4 | DISCUSSION

4.1 | Interspecific variability of the traits studied

Among the traits we examined, the most noticeable differences among species manifested within traits related to the dry biomass of flowers and fruits, while the most stable traits pertained to carbon content in flowers and leaves. The significant heterogeneity in the dry mass of flowers and fruits across the surveyed species can be attributed to the adaptation to diverse pollination and dispersal mechanisms. The broad diversity of flower forms, which includes not only morphological structures but also dimensions, can result from various selection agents, including selective herbivores, abiotic factors, mutualistic interactions with other organisms such as fungi, and, to a significant extent, varied pollination factors (Chanderbali et al., 2016; Chartier et al., 2021). For instance, the categorization of species into insect- and wind-pollinated explains the observed diversity (Armbruster et al., 2000; Sapir et al., 2019). Wind-pollinated species, for example oaks or pines, do not have a justification to expend resources on the costly production of large-volume, distinct flowers, given their high abundance of airborne pollen. Conversely, species engaged in competition for pollinators, such as *Magnolia* spp. or *Cornus* spp., necessitate more showy or fragrant flowers to be more attractive than competing species, thereby driving further diversification in morphological structures of flowers.

Similarly, concerning fruits, whose dimensions often correlate with those of flowers, their fundamental role remains consistent: to facilitate the successful reproduction of the specimen (Kourmpetli & Drea, 2014). However, the strategies employed to realize this objective vary markedly among species. Some fruits, as in willows, necessitate reduction in mass for anemochoric dispersal, while others require substantial mass to benefit from the

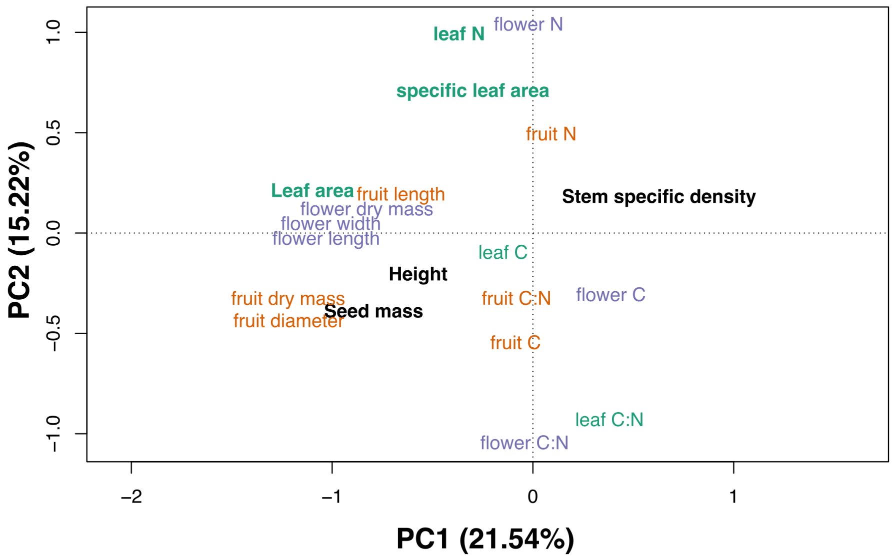
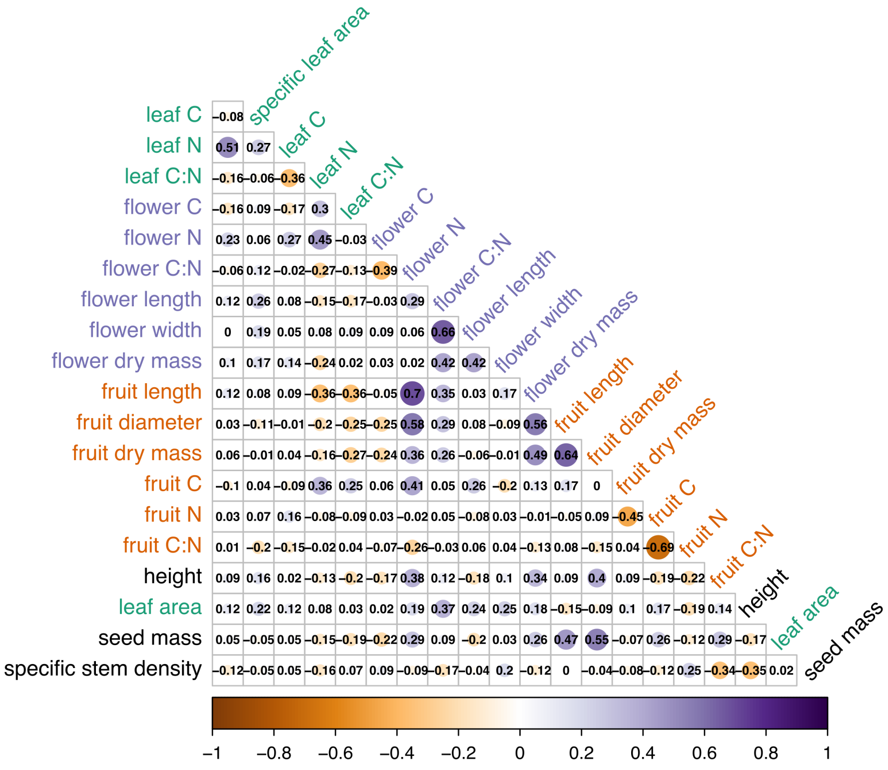


FIGURE 4 Results of principal components analysis comparing well-established traits from the global spectrum of plant form and function (in bold) and lesser-recognized traits proposed in this study. Purple labels represent floral traits, orange labels – fruit traits, and green labels – leaf traits. Black labels indicate traits from the global spectrum of plant form and function, values of which were derived from the TRY database (see Section 2.4) (Kattge et al., 2020).



	specific leaf area	leaf C	leaf N	leaf C:N	flower C	flower N	flower C:N	flower length	flower width	flower dry mass	fruit length	fruit diameter	fruit dry mass	fruit C	fruit N	fruit C:N	height	leaf area	seed mass
leaf C	−0.08																		
leaf N	0.51	0.27																	
leaf C:N	−0.16	−0.06	−0.36																
flower C	−0.16	0.09	−0.17	0.3															
flower N	0.23	0.06	0.27	0.45	−0.03														
flower C:N	−0.06	0.12	−0.02	−0.27	−0.13	−0.39													
flower length	0.12	0.26	0.08	−0.15	−0.17	−0.03	0.29												
flower width	0	0.19	0.05	0.08	0.09	0.09	0.06	0.66											
flower dry mass	0.1	0.17	0.14	−0.24	0.02	0.03	0.02	0.42	0.42										
fruit length	0.12	0.08	0.09	−0.36	−0.36	−0.05	0.7	0.35	0.03	0.17									
fruit diameter	0.03	−0.11	−0.01	−0.2	−0.25	−0.25	0.58	0.29	0.08	−0.09	0.56								
fruit dry mass	0.06	−0.01	0.04	−0.16	−0.27	−0.24	0.36	0.26	−0.06	−0.01	0.49	0.64							
fruit C	−0.1	0.04	−0.09	0.36	0.25	0.06	0.41	0.05	0.26	−0.2	0.13	0.17	0						
fruit N	0.03	0.07	0.16	−0.08	−0.09	0.03	−0.02	0.05	−0.08	0.03	−0.01	−0.05	0.09	−0.45					
fruit C:N	0.01	−0.2	−0.15	−0.02	0.04	−0.07	−0.26	−0.03	0.06	0.04	−0.13	0.08	−0.15	0.04	−0.69				
height	0.09	0.16	0.02	−0.13	−0.2	−0.17	0.38	0.12	−0.18	0.1	0.34	0.09	0.4	0.09	−0.19	−0.22			
leaf area	0.12	0.22	0.12	0.08	0.03	0.02	0.19	0.37	0.24	0.25	0.18	−0.15	−0.09	0.1	0.17	−0.19	0.14		
seed mass	0.05	−0.05	0.05	−0.15	−0.19	−0.22	0.29	0.09	−0.2	0.03	0.26	0.47	0.55	−0.07	0.26	−0.12	0.29	−0.17	
specific stem density	−0.12	−0.05	0.05	−0.16	0.07	0.09	−0.09	−0.17	−0.04	0.2	−0.12	0	−0.04	−0.08	−0.12	0.25	−0.34	−0.35	0.02

FIGURE 5 Correlation matrix describing the strength of bivariate relationships between each pair of traits, calculated accounting for phylogenetic dependence of species via the corphylo function from the ape package (Paradis & Schliep, 2019), expressed as Pearson's correlation coefficients (*r*). Purple labels represent floral traits, orange labels – fruit traits, and green labels – leaf traits. Black labels indicate traits from the global spectrum of plant form and function, values of which were derived from the TRY database (see Section 2.4) (Kattge et al., 2020).

proximity to the maternal tree, or from the resources provided, as in *Aesculus* spp. or *Quercus* spp. Furthermore, the structural composition of fruits, whether categorized as dry or fleshy, is intrinsically linked to the species' reproductive strategy. Fleshy fruits, for instance, serve to attract herbivores and facilitate seed dispersal by endozoochory, often concurrently providing essential resources for the seed after dispersion through animal excretion, as in *Prunus* spp. Conversely, dry fruits predominantly serve as a protective barrier for the seed against external agents, given that the seed frequently already harbors the requisite resources for germination, as in *Juglans* spp. The expansive array of pollination mechanisms and reproductive strategies constitutes a plausible rationale for the considerable variability observed in flower and fruit dry biomass.

As species with different ecological strategies can exhibit different carbon allocation patterns (Grasset et al., 2015; Trugman et al., 2019), we might expect varying carbon allocation patterns in flowers, fruits, and leaves across the species analyzed. However, in our study, we observed minimal variability of carbon content across these three organs. When examining the stability of traits linked to carbon content in plant organs, we can attribute it to the fundamental role of carbon as a building block. Carbon forms the basis of the main structural components of plant cells. For example, cellulose, the primary component of plant cell walls, consists of carbon, hydrogen, and oxygen (McFarlane et al., 2014). Similarly, lignin, another crucial structural element, provides strength to cell walls and also contains carbon (Neutelings, 2011). As a result, the consistent presence of carbon in plant organs displays limited variability.

In contrast, nitrogen content, especially in fruits, exhibits a higher level of variability compared to carbon. This variability can be attributed to the pivotal role of nitrogen in amino acids, the essential building blocks of proteins (Atilio & Causin, 1996). Since nitrogen is a critical nutrient for plants, its deficiency triggers a series of physiological and biochemical responses aimed at efficient nitrogen acquisition and utilization (Ye et al., 2022). These responses include reduced growth (Broadley et al., 2000), delayed development (Ma et al., 1997), and changes in the allocation of resources (Mu & Chen, 2021). In response to nitrogen deficiency, plants strategically redistribute resources, prioritizing essential functions (Zhao et al., 2005). For instance, nitrogen is reallocated from older leaves to younger, actively growing tissues, ensuring that the limited nitrogen is directed toward critical physiological processes (Ueda et al., 2011). This dynamic response highlights the plant's adaptability in optimizing resource utilization under varying nitrogen conditions.

4.2 | Intraspecimen variability of the traits studied

At the intraspecimen level, our investigation highlighted SLA as the most variable trait, contrasting with the overall stability observed in carbon content across all three examined organs, consistent with interspecific analyses. While prior studies have acknowledged the high variability of SLA within individual specimens (Gunn et al., 1999; Paź-Dyderska et al., 2020), it is essential to underscore the substantial difference in its variability compared to other traits tested. SLA is a valuable indicator of resource availability. Therefore, it can vary significantly even within a single specimen. This dynamic adaptability of SLA stems from leaves adjusting to varying light availability, leading to observable changes in SLA values (Legner et al., 2014; Poorter et al., 2006; Reich et al., 1998).

Leaves, functioning as the primary assimilation apparatus of plants, play a pivotal role in photosynthesis, utilizing light, carbon dioxide, and water to synthesize glucose and other carbohydrates (Crang et al., 2018). These carbohydrates not only act as an energy source for diverse plant activities but also serve as fundamental building blocks for various organic compounds. Consequently, changes in light availability prompt adaptive responses in SLA, optimizing resource utilization (Gratani et al., 2006; James & Bell, 2000; Wyka et al., 2012). In contrast, flowers and fruits, reliant on the photosynthetic products generated by leaf activity, may not exhibit as pronounced a response to changes in light availability (but see Garrido et al., 2023). Their stability in the face of varying light conditions can be attributed to their dependency on the consistent products of photosynthesis provided by leaves. It is worth noting that the potential impact of light availability on flowers might be further diminished by considering that several species blossom before the development of leaves (Tal, 2011).

Yet, we have still identified significant intracanopy variability for both flowers and fruits, with flower and fruit dry biomass emerging as the second and third most variable traits in our analysis. This variability could be ascribed to intentional placement strategies employed by woody species for their flowers and fruits within the canopy. The deliberate positioning of flowers is especially vital due to its key role in ensuring successful pollination, subsequently influencing fruit and seed production (Khalil et al., 2023). Additionally, the location of flowers can be influenced by the imperative need to attract specific pollinators (Damascena et al., 2017). Some trees place their flowers in visible and accessible positions to enhance the probability of attracting pollinators.

Similarly, the positioning of fruits within the canopy contributes to intracanopy variability of various fruit parameters. For example, light exposure can significantly affect fruit quality, as demonstrated in various *Malus × domestica* cultivars. In apples, fruits from the outer canopy exhibited higher fresh weight and soluble solids content compared to those from the inner canopy. Additionally, the outer-canopy fruits had higher concentrations of soluble sugars and sugar alcohols, but lower starch concentrations (Feng et al., 2014). Nilsson and Gustavsson (2007) similarly found that fruits developing outside the canopy acquired a red peel color during maturation, while those inside remained green. Outside fruits had higher contents of dry matter, soluble solids, and soluble sugars, but lower amounts of titratable acidity than inside fruits. According to the results of Tustin et al. (1988), both fresh weight and soluble solids concentration showed highly positive correlations with the transmission of photosynthetic photon flux. Consequently, fruit fresh weight and soluble solids concentration increased with increasing height in the canopy and were higher in the outer canopy position.

Intracanopy variability in fruits may arise because those in the upper canopy receive more direct sunlight, promoting enhanced photosynthesis and facilitating optimal fruit ripening (Khalil et al., 2023). This is particularly crucial for tree species reliant on sunlight for the initiation and completion of the ripening process, such as trees of *Malus* spp. or *Prunus* spp. Moreover, some trees employ a strategy of placing fruits at higher positions within the canopy to capitalize on wind dispersal (Qin et al., 2022). Elevated fruits are more likely to be caught by the wind, facilitating their dispersal away from the parent tree and increasing the likelihood of successful seed dispersal and colonization in new areas (Qin et al., 2022). While these active strategies employed by trees and shrubs underscore the variability observed in flower and fruit traits in our study, a comprehensive understanding of the factors influencing such variations would require further studies.

4.3 | Potential of the floral and fruit traits in functional ecology

In examining the potential of floral and fruit traits in functional ecology, our study establishes connections between the newly proposed traits and the widely recognized traits delineated by Díaz and co-authors (Díaz et al., 2016). Employing six traits from the global spectrum of plant form and function, our PCA revealed two axes of variation within the species pool: one reflecting a size-related variability of traits and the second, explaining variability in chemical composition of the studied plants.

While our novel floral and fruit traits don't introduce new dimensions to the variability already explained by the six traits proposed by Díaz et al. (2016), their significance lies in their alignment with the established traits. This alignment underscores the potential for predicting floral and fruit traits based on the well-recognized traits from Díaz et al. (2016). For instance, our results suggest that species with high leaf area and seed mass values are likely to exhibit flowers and fruits with higher dry biomass and larger size. Also, based on the analysis of bivariate correlations, we observed a positive correlation between seed mass, fruit diameter, and fruit dry biomass. However, these results contrast with those of Bentos et al. (2014), who identified a positive correlation between the number of seeds per fruit and fruit mass, but a negative correlation with seed mass. This disparity may be attributed to the different life strategies exhibited by the species studied, particularly since the discussed study focused on pioneer tree species of the Amazon forest. In our results, we also found a positive correlation between seed mass and height, consistent with the well-established findings of Díaz et al. (2016). Notably, the size-related traits of both flowers and fruits showed significant overlap, indicating a potential correlation between the sizes of these organs. This idea could be supported by early work on the topic of coordination between traits related to organ or organism size (Ackerly & Donoghue, 1998; Bond & Midgley, 1988; Corner, 1949), often referred to as Corner's rules. In contrast, SLA did not align as strongly within the size-related traits, possibly due to its robust correlation with leaf nitrogen content, a relationship well-documented in prior studies (Díaz et al., 2016; Reich et al., 1998; Wright et al., 2004).

In summary, while our novel traits don't contribute new dimensions to the understanding of plant form and function variability, they align effectively within existing dimensions. This alignment offers the potential to predict floral- and fruit-related traits, and consequently, plant reproductive strategies, based on more established and readily available plant functional traits. However, this predictive capacity necessitates further studies incorporating data from a broader array of species.

4.4 | Study limitations

During the initial phase of our study, we carefully weighed trade-offs that introduced particular limitations. To ensure a broader diversity of species in our research, we opted to include only one representative specimen per species. While there is no universally determined optimal sample size for studying the intraspecific variability of flowers, existing research on foliar traits suggests that the most accurate sampling size involves four samples from 10 individuals (Petruzzellis et al., 2017). Despite recognizing that a larger number of specimens would offer a more comprehensive representation of data variability, we chose to concentrate on collecting flowers from individual specimens. This decision was influenced not only by the Arboretum's layout, where frequently only one mature specimen of each species is present, but also by the labor-intensive nature of data collection.

The dynamic nature of flowering, occurring at various times throughout the growing season, rendered it impractical to collect data at a single time point, unlike leaves that remain accessible for months during the vegetative season. Additionally, we acknowledge that flowers, akin to other plant organs, undergo seasonal variations in their chemical composition, encompassing both the C and N contents analyzed in our study and other compounds (Ernst et al., 1991; Kenis et al., 1985; McMann et al., 2022). Nevertheless, our investigation stands as one of the pioneering efforts to explore the potential of C and N content in flowers for applications in the field of functional ecology. As a result, we consciously chose to temporarily set aside consideration of this type of variability, deeming it of minimal significance at this stage of the field's development. To standardize results we decided to sample organs of each species in the optimum of their development.

We encountered challenges in collecting fruits from the specimens under study, as certain species did not produce fruits. As detailed in the Section 2, this phenomenon could be attributed to the year-to-year variability in environmental conditions or the insufficient number of male specimens capable of fertilization in certain dioecious species. Additionally, herbivory was prevalent, leading to the consumption of many fruits by birds before reaching full ripening. Despite these challenges, as one of the pioneering studies of its kind, we believe that the innovative nature of the research can contribute to addressing specific limitations. Nevertheless, we emphasize that further studies, incorporating data not only from a greater variety of species but also from numerous specimens of the same species, are crucial for a more in-depth exploration of intraspecific trait variability of reproductive organs.

5 | CONCLUSIONS

Our objective was to contribute to the dynamic field of functional ecology, specifically in relation to reproductive organs – flowers and fruits. To achieve this, we introduced floral and fruit traits that had been previously overlooked, employing a quantitative approach to assess their variability. Our investigation involved exploration of the variability and stability of these newly introduced traits, concentrating on 12 quantitative traits that offer insights into the reproductive strategies of woody species. Despite the development of studies on floral and fruit functional traits over the last years, comparative analyses of the variability in these traits with established ones are rare, if not absent. Through our analysis, we unveiled significant interspecific variability across these traits, exposing a broad spectrum of diversity among the studied species. We delved into intraspecific differences, revealing a limited level of variation within individual specimens. Furthermore, we investigated correlations between these traits and widely utilized traits from the global spectrum of plant form and function proposed by Díaz et al. (2016), uncovering intriguing connections between the established traits and the floral and fruit traits upon which we focused, and complementing the already well-recognized variability in plant form and function with additional insights into reproductive processes.

AUTHOR CONTRIBUTIONS

Sonia Paź-Dyderska: Conceptualization (equal); data curation (lead); formal analysis (lead); funding acquisition (equal); investigation (lead); methodology (equal); project administration (lead); software (lead); validation (lead); visualization (lead); writing – original draft (lead). **Andrzej M. Jagodziński:** Conceptualization (equal); funding acquisition (equal); methodology (equal); supervision (lead); writing – review and editing (lead).

ACKNOWLEDGMENTS

We would like to thank Kinga Nowak for her invaluable assistance in the selection of species that align with the goals of our research. We express our appreciation to Marcin K. Dyderski for his insightful and constructive feedback on the manuscript. We are grateful to two anonymous reviewers for their valuable comments, which have significantly contributed to the improvement of the manuscript.

FUNDING INFORMATION

The study was financed by the National Science Centre, Poland, as part of Project No. 2020/37/N/NZ8/00387 titled: “How to better describe the functioning of species in an ecosystem? Reproduction traits and their potential in functional ecology of plants.” The study was partially supported by the Institute of Dendrology of the Polish Academy of Sciences.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in figshare at https://doi.org/10.6084/m9.figshare.25204934.v1.

ORCID

Sonia Paź-Dyderska https://orcid.org/0000-0001-9634-7479
Andrzej M. Jagodziński https://orcid.org/0000-0001-6899-0985

REFERENCES

Acevedo-Quintero, J.-F., Zamora-Abrego, J.-G., Chica-Vargas, J.-P., & Mancera-Rodríguez, N.-J. (2023). Functional traits of fruits of particular importance for seed dispersers in the tropical dry forest. *Revista de Biología Tropical*, *71*, e52288. https://doi.org/10.15517/rev.biol.trop..v71i1.52288

Ackerly, D. D., & Donoghue, M. J. (1998). Leaf size, sapling allometry, and Corner's rules: Phylogeny and correlated evolution in maples (*Acer*). *The American Naturalist*, *152*, 767–791. https://doi.org/10.1086/286208

Adler, P. B., Salguero-Gómez, R., Compagnoni, A., Hsu, J. S., Ray-Mukherjee, J., Mbeau-Ache, C., & Franco, M. (2014). Functional traits explain variation in plant life history strategies. *Proceedings of the National Academy of Sciences of the United States of America*, *111*, 740–745. https://doi.org/10.1073/pnas.1315179111

Agrawal, A. A. (2020). A scale-dependent framework for trade-offs, syndromes, and specialization in organismal biology. *Ecology*, *101*, e02924. https://doi.org/10.1002/ecy.2924

Anderson, G. J., & Hill, J. D. (2002). Many to flower, few to fruit: The reproductive biology of *Hamamelis virginiana* (Hamamelidaceae). *American Journal of Botany*, *89*, 67–78. https://doi.org/10.3732/ajb.89.1.67

Armbruster, S., Fenster, C., & Dudash, M. (2000). Pollination “principles” revisited: Specialization, pollination syndromes, and the evolution of flowers. *The Scandinavian Association for Pollination Ecology Honours Knut Faegri*, *39*, 179–200.

Ashman, T.-L., & Schoen, D. J. (1996). Floral longevity: Fitness consequences and resource costs. In D. G. Lloyd & S. C. H. Barrett (Eds.), *Floral biology: Studies on floral evolution in animal-pollinated plants* (pp. 112–139). Springer US. https://doi.org/10.1007/978-1-4613-1165-2_5

Atilio, B. J., & Causin, H. F. (1996). The central role of amino acids on nitrogen utilization and plant growth. *Journal of Plant Physiology*, *149*, 358–362. https://doi.org/10.1016/S0176-1617(96)80134-9

Aun, M. A., Farnese, F., Loram-Lourenço, L., de Abreu, I. M. P. G., Silva, B. R. A., Freitas, J. C. E., Filho, V. M. A., Silva, F. G., Franco, A. C., Hammond, W. M., Cochard, H., & Menezes-Silva, P. E. (2024). Evidence of combined flower thermal and drought vulnerabilities portends reproductive failure under hotter-drought conditions. *Plant, Cell & Environment*, *47*, 1971–1986. https://doi.org/10.1111/pce.14857

Bardgett, R. D., Mommer, L., & De Vries, F. T. (2014). Going underground: Root traits as drivers of ecosystem processes. *Trends in Ecology & Evolution*, *29*, 692–699. https://doi.org/10.1016/j.tree.2014.10.006

Bentos, T. V., Mesquita, R. C. G., Camargo, J. L. C., & Williamson, G. B. (2014). Seed and fruit tradeoffs – The economics of seed packaging in Amazon pioneers. *Plant Ecology and Diversity*, *7*, 371–382. https://doi.org/10.1080/17550874.2012.740081

Birkhold, K. T., Koch, K. E., & Darnell, R. L. (1992). Carbon and nitrogen economy of developing Rabbiteye blueberry fruit. *Journal of the American Society for Horticultural Science*, *117*, 139–145.

Bolmgren, K., & Eriksson, O. (2005). Fleshy fruits – Origins, niche shifts, and diversification. *Oikos*, *109*, 255–272. https://doi.org/10.1111/j.0030-1299.2005.12663.x

Bond, W. J., & Midgley, J. (1988). Allometry and sexual differences in leaf size. *The American Naturalist*, *131*, 901–910. https://doi.org/10.1086/284830

Bosch, J., Retana, J., & Cerdá, X. (1997). Flowering phenology, floral traits and pollinator composition in a herbaceous Mediterranean plant community. *Oecologia*, *109*, 583–591. https://doi.org/10.1007/s004420050120

Broadley, M. R., Escobar-Gutiérrez, A. J., Burns, A., & Burns, I. G. (2000). What are the effects of nitrogen deficiency on growth components of lettuce? *New Phytologist*, *147*, 519–526. https://doi.org/10.1046/j.1469-8137.2000.00715.x

Bussotti, F., Pollastrini, M., Holland, V., & Brüggemann, W. (2015). Functional traits and adaptive capacity of European forests to climate change. *Environmental and Experimental Botany*, *111*, 91–113. https://doi.org/10.1016/j.envexpbot.2014.11.006

Cedro, A., & Iszkuło, G. (2011). Do females differ from males of European yew (*Taxus baccata* L.) in dendrochronological analysis? *Tree-Ring Research*, *67*, 3–11. https://doi.org/10.3959/2009-9.1

Chai, Y., Yue, M., Wang, M., Xu, J., Liu, X., Zhang, R., & Wan, P. (2016). Plant functional traits suggest a change in novel ecological strategies for dominant species in the stages of forest succession. *Oecologia*, *180*, 771–783. https://doi.org/10.1007/s00442-015-3483-3

Chanderbali, A. S., Berger, B. A., Howarth, D. G., Soltis, P. S., & Soltis, D. E. (2016). Evolving ideas on the origin and evolution of flowers:

New perspectives in the genomic era. *Genetics*, *202*, 1255–1265. https://doi.org/10.1534/genetics.115.182964

Chartier, M., Löfstrand, S., von Balthazar, M., Gerber, S., Jabbour, F., Sauquet, H., & Schönenberger, J. (2017). How (much) do flowers vary? Unbalanced disparity among flower functional modules and a mosaic pattern of morphospace occupation in the order Ericales. *Proceedings of the Royal Society B: Biological Sciences*, *284*, 20170066. https://doi.org/10.1098/rspb.2017.0066

Chartier, M., von Balthazar, M., Sontag, S., Löfstrand, S., Palme, T., Jabbour, F., Sauquet, H., & Schönenberger, J. (2021). Global patterns and a latitudinal gradient of flower disparity: Perspectives from the angiosperm order Ericales. *New Phytologist*, *230*, 821–831. https://doi.org/10.1111/nph.17195

Cordlandwehr, V., Meredith, R. L., Ozinga, W. A., Bekker, R. M., Groenendael, J. M. v., & Bakker, J. P. (2013). Do plant traits retrieved from a database accurately predict on-site measurements? *Journal of Ecology*, *101*, 662–670. https://doi.org/10.1111/1365-2745.12091

Corner, E. J. H. (1949). The durian theory or the origin of the modern tree. *Annals of Botany*, *13*, 367–414.

Cornwell, W. K., Pearse, W. D., Dalrymple, R. L., & Zanne, A. E. (2019). What we (don't) know about global plant diversity. *Ecography*, *42*, 1819–1831. https://doi.org/10.1111/ecog.04481

Crang, R., Lyons-Sobaski, S., & Wise, R. (2018). Leaves. In R. Crang, S. Lyons-Sobaski, & R. Wise (Eds.), *Plant anatomy: A concept-based approach to the structure of seed plants* (pp. 395–441). Springer International Publishing. https://doi.org/10.1007/978-3-319-77315-5_12

Cresswell, J. E. (1998). Stabilizing selection and the structural variability of flowers within species. *Annals of Botany*, *81*, 463–473. https://doi.org/10.1006/anbo.1998.0594

Damascena, J. G., Leite, G. L. D., Silva, F. W. S., Soares, M. A., Guanabens, R. E. M., Sampaio, R. A., & Zanuncio, J. C. (2017). Spatial distribution of phytophagous insects, natural enemies, and pollinators on *Leucaena leucocephala* (Fabaceae) trees in the Cerrado. *Florida Entomologist*, *100*, 558–565. https://doi.org/10.1653/024.100.0311

de Paz, M., Gobbi, M. E., & Raffaele, E. (2018). Fallen fruits stimulate decomposition of leaf litter of dominant species in NW Patagonia shrublands. *Plant and Soil*, *425*, 433–440. https://doi.org/10.1007/s11104-018-3590-0

Díaz, S., & Cabido, M. R. (2001). Vive la différence: Plant functional diversity matters to ecosystem processes. *Trends in Ecology & Evolution*, *16*, 646–655. https://doi.org/10.1016/S0169-5347(01)02283-2

Díaz, S., Kattge, J., Cornelissen, J. H. C., Wright, I. J., Lavorel, S., Dray, S., Reu, B., Kleyer, M., Wirth, C., Colin Prentice, I., Garnier, E., Bönisch, G., Westoby, M., Poorter, H., Reich, P. B., Moles, A. T., Dickie, J., Gillison, A. N., Zanne, A. E., … Gorné, L. D. (2016). The global spectrum of plant form and function. *Nature*, *529*, 167–171. https://doi.org/10.1038/nature16489

Dosmann, M., & Groover, A. (2012). The importance of living botanical collections for plant biology and the "next generation" of evo-devo research. *Frontiers in Plant Science*, *3*, 137. https://doi.org/10.3389/fpls.2012.00137

Dylewski, Ł., Adamczyk, D., Żytkowiak, R., & Jagodziński, A. M. (2024). Seed mass and seed resources – Testing the defense trade-off hypothesis in woody plants. *Dendrobiology*, *91*, 32–41. https://doi.org/10.12657/denbio.091.003

Edwards, C. E., Bassüner, B., Birkinshaw, C., Camara, C., Lehavana, A., Lowry, P. P., Miller, J. S., Wyatt, A., & Jackson, P. W. (2018). A botanical mystery solved by phylogenetic analysis of botanical garden collections: The rediscovery of the presumed-extinct *Dracaena umbraculifera*. *Oryx*, *52*, 427–436. https://doi.org/10.1017/S0030605317001570

Ernst, W. H. O., Kuiters, A. T., Nelissen, H. J. M., & Tolsma, D. J. (1991). Seasonal variation in phenolics in several savanna tree species in Botswana. *Acta Botanica Neerlandica*, *40*, 63–74. https://doi.org/10.1111/j.1438-8677.1991.tb01514.x

E-Vojtkó, A., de Bello, F., Durka, W., Kühn, I., Götzenberger, L. (2020). The neglected importance of floral traits in trait-based plant community assembly. *Journal of Vegetation Science*, *31*, 529–539. https://doi.org/10.1111/jvs.12877

E-Vojtkó, A., Junker, R. R., de Bello, F., & Götzenberger, L. (2022). Floral and reproductive traits are an independent dimension within the plant economic spectrum of temperate central Europe. *New Phytologist*, *236*, 1964–1975. https://doi.org/10.1111/nph.18386

Fanal, A., Mahy, G., Fayolle, A., & Monty, A. (2021). Arboreta reveal the invasive potential of several conifer species in the temperate forests of western Europe. *NeoBiota*, *64*, 23–42. https://doi.org/10.3897/neobiota.64.56027

Faraji, L., & Karimi, M. (2022). Botanical gardens as valuable resources in plant sciences. *Biodiversity and Conservation*, *31*, 2905–2926. https://doi.org/10.1007/s10531-019-01926-1

Farré-Armengol, G., Filella, I., Llusia, J., & Peñuelas, J. (2013). Floral volatile organic compounds: Between attraction and deterrence of visitors under global change. *Perspectives in Plant Ecology, Evolution and Systematics*, *15*, 56–67. https://doi.org/10.1016/j.ppees.2012.12.002

Feltz, C. J., & Miller, G. E. (1996). An asymptotic test for the equality of coefficients of variation from k populations. *Statistics in Medicine*, *15*, 647–658. https://doi.org/10.1002/(SICI)1097-0258(19960330)15:6<647::AID-SIM184>3.0.CO;2-P

Feng, F., Li, M., Ma, F., & Cheng, L. (2014). Effects of location within the tree canopy on carbohydrates, organic acids, amino acids and phenolic compounds in the fruit peel and flesh from three apple (*Malus × domestica*) cultivars. *Horticulture Research*, *1*, 1–7. https://doi.org/10.1038/hortres.2014.19

Funk, J. L. (2008). Differences in plasticity between invasive and native plants from a low resource environment. *Journal of Ecology*, *96*, 1162–1173. https://doi.org/10.1111/j.1365-2745.2008.01435.x

Garrido, A., Conde, A., Serôdio, J., De Vos, R. C. H., & Cunha, A. (2023). Fruit photosynthesis: More to know about where, how and why. *Plants*, *12*, 2393. https://doi.org/10.3390/plants12132393

Gavini, S. S., Quintero, C., & Tadey, M. (2018). Predator and floral traits change pollinator behaviour, with consequences for plant fitness. *Ecological Entomology*, *43*, 731–741. https://doi.org/10.1111/een.12659

Gómez, J. M., Torices, R., Lorite, J., Klingenberg, C. P., & Perfectti, F. (2016). The role of pollinators in the evolution of corolla shape variation, disparity and integration in a highly diversified plant family with a conserved floral bauplan. *Annals of Botany*, *117*, 889–904. https://doi.org/10.1093/aob/mcv194

Grasset, C., Delolme, C., Arthaud, F., & Bornette, G. (2015). Carbon allocation in aquatic plants with contrasting strategies: The role of habitat nutrient content. *Journal of Vegetation Science*, *26*, 946–955. https://doi.org/10.1111/jvs.12298

Gratani, L., Covone, F., & Larcher, W. (2006). Leaf plasticity in response to light of three evergreen species of the Mediterranean maquis. *Trees*, *20*, 549–558. https://doi.org/10.1007/s00468-006-0070-6

Guerrero-Ramírez, N. R., Mommer, L., Freschet, G. T., Iversen, C. M., McCormack, M. L., Kattge, J., Poorter, H., van der Plas, F., Bergmann, J., Kuyper, T. W., York, L. M., Bruelheide, H., Laughlin, D. C., Meier, I. C., Roumet, C., Semchenko, M., Sweeney, C. J., van Ruijven, J., Valverde-Barrantes, O. J., … Weigelt, A. (2021). Global root traits (GRooT) database. *Global Ecology and Biogeography*, *30*, 25–37. https://doi.org/10.1111/geb.13179

Gunn, S., Farrar, J. F., Collis, B. E., & Nason, M. (1999). Specific leaf area in barley: Individual leaves versus whole plants. *New Phytologist*, *143*, 45–51. https://doi.org/10.1046/j.1469-8137.1999.00434.x

Heberling, J. M., Cassidy, S. T., Fridley, J. D., & Kalisz, S. (2019). Carbon gain phenologies of spring-flowering perennials in a deciduous forest indicate a novel niche for a widespread invader. *New Phytologist*, *221*, 778–788. https://doi.org/10.1111/nph.15404

Holm, S. (1979). A simple sequentially rejective multiple test procedure. *Scandinavian Journal of Statistics*, *6*, 65–70.

Intergovernmental Panel on Climate Change. (2023). *Climate change 2022 – Impacts, adaptation and vulnerability: Working group II contribution to the sixth assessment report of the intergovernmental panel on climate change*. Cambridge University Press. https://doi.org/10.1017/9781009325844

Iversen, C. M., McCormack, M. L., Powell, A. S., Blackwood, C. B., Freschet, G. T., Kattge, J., Roumet, C., Stover, D. B., Soudzilovskaia, N. A., Valverde-Barrantes, O. J., van Bodegom, P. M. v., & Violle, C. (2017). A global fine-root ecology database to address belowground challenges in plant ecology. *New Phytologist*, *215*, 15–26. https://doi.org/10.1111/nph.14486

James, S. A., & Bell, D. T. (2000). Influence of light availability on leaf structure and growth of two *Eucalyptus globulus* ssp. *globulus* provenances. *Tree Physiology*, *20*, 1007–1018. https://doi.org/10.1093/treephys/20.15.1007

Jin, Y., & Qian, H. (2022). V.PhyloMaker2: An updated and enlarged R package that can generate very large phylogenies for vascular plants. *Plant Diversity*, *44*, 335–339. https://doi.org/10.1016/j.pld.2022.05.005

Johnson, T. F., Isaac, N. J. B., Paviolo, A., & González-Suárez, M. (2021). Handling missing values in trait data. *Global Ecology and Biogeography*, *30*, 51–62. https://doi.org/10.1111/geb.13185

Junker, R. R., & Parachnowitsch, A. L. (2015). Working towards a holistic view on flower traits—How floral scents mediate plant–animal interactions in concert with other floral characters. *Journal of the Indian Institute of Science*, *95*, 43–68.

Kattenborn, T., Fassnacht, F. E., Pierce, S., Lopatin, J., Grime, J. P., & Schmidtlein, S. (2017). Linking plant strategies and plant traits derived by radiative transfer modelling. *Journal of Vegetation Science*, *28*, 717–727. https://doi.org/10.1111/jvs.12525

Kattge, J., Bönisch, G., Díaz, S., Lavorel, S., Prentice, I. C., Leadley, P., Tautenhahn, S., Werner, G. D. A., Aakala, T., Abedi, M., Acosta, A. T. R., Adamidis, G. C., Adamson, K., Aiba, M., Albert, C. H., Alcántara, J. M., Carolina Alcázar, C., Aleixo, I., Ali, H., … Wirth, C. (2020). TRY plant trait database – Enhanced coverage and open access. *Global Change Biology*, *26*, 119–188. https://doi.org/10.1111/gcb.14904

Kenis, J. D., Silvente, S. T., & Trippi, V. S. (1985). Nitrogen metabolism and senescence-associated changes during growth of carnation flowers. *Physiologia Plantarum*, *65*, 455–459. https://doi.org/10.1111/j.1399-3054.1985.tb08673.x

Khalil, A., Mir, M., Nabi, S., Mir, M. M., Iqbal, U., Nazir, N., Banday, S. A., Bhat, R., Khan, S. Q., & Wani, T. F. (2023). Canopy management. In M. M. Mir, M. U. Rehman, U. Iqbal, & S. A. Mir (Eds.), *Temperate nuts* (pp. 209–245). Springer Nature. https://doi.org/10.1007/978-981-19-9497-5_9

Kleyer, M., & Minden, V. (2015). Why functional ecology should consider all plant organs: An allocation-based perspective. *Basic and Applied Ecology*, *16*, 1–9. https://doi.org/10.1016/j.baae.2014.11.002

Kourmpetli, S., & Drea, S. (2014). The fruit, the whole fruit, and everything about the fruit. *Journal of Experimental Botany*, *65*, 4491–4503. https://doi.org/10.1093/jxb/eru144

Krishnamoorthy, K., & Lee, M. (2014). Improved tests for the equality of normal coefficients of variation. *Computational Statistics*, *29*, 215–232. https://doi.org/10.1007/s00180-013-0445-2

Kühn, N., Tovar, C., Carretero, J., Vandvik, V., Enquist, B. J., & Willis, K. J. (2021). Globally important plant functional traits for coping with climate change. *Frontiers of Biogeography*, *13*(4), e53774. https://doi.org/10.21425/F5FBG53774

Lambrecht, S. C. (2013). Floral water costs and size variation in the highly selfing *Leptosiphon bicolor* (Polemoniaceae). *International Journal of Plant Sciences*, *174*, 74–84. https://doi.org/10.1086/668230

Laughlin, D. C. (2014). The intrinsic dimensionality of plant traits and its relevance to community assembly. *Journal of Ecology*, *102*, 186–193. https://doi.org/10.1111/1365-2745.12187

Laughlin, D. C., Joshi, C., van Bodegom, P. M., Bastow, Z. A., & Fulé, P. Z. (2012). A predictive model of community assembly that incorporates intraspecific trait variation. *Ecology Letters*, *15*, 1291–1299. https://doi.org/10.1111/j.1461-0248.2012.01852.x

Laughlin, D. C., Leppert, J. J., Moore, M. M., & Sieg, C. H. (2010). A multi-trait test of the leaf-height-seed plant strategy scheme with 133 species from a pine forest flora. *Functional Ecology*, *24*, 493–501. https://doi.org/10.1111/j.1365-2435.2009.01672.x

Lavorel, S., & Garnier, E. (2002). Predicting changes in community composition and ecosystem functioning from plant traits: Revisiting the holy grail. *Functional Ecology*, *16*, 545–556. https://doi.org/10.1046/j.1365-2435.2002.00664.x

Legner, N., Fleck, S., & Leuschner, C. (2014). Within-canopy variation in photosynthetic capacity, SLA and foliar N in temperate broad-leaved trees with contrasting shade tolerance. *Trees*, *28*, 263–280. https://doi.org/10.1007/s00468-013-0947-0

Levey, D. J., Bissell, H. A., & O'Keefe, S. F. (2000). Conversion of nitrogen to protein and amino acids in wild fruits. *Journal of Chemical Ecology*, *26*, 1749–1763. https://doi.org/10.1023/A:1005503316406

Liu, C., Li, Y., Yan, P., & He, N. (2021). How to improve the predictions of plant functional traits on ecosystem functioning? *Frontiers in Plant Science*, *12*, 622260. https://doi.org/10.3389/fpls.2021.622260.

Lussu, M., De Agostini, A., Cogoni, A., Marignani, M., & Cortis, P. (2019). Does size really matter? A comparative study on floral traits in orchids with two different pollination strategies. *Plant Biology*, *21*, 961–966. https://doi.org/10.1111/plb.12993

Ma, Q., Longnecker, N., & Dracup, M. (1997). Nitrogen deficiency slows leaf development and delays flowering in narrow-leafed lupin. *Annals of Botany*, *79*, 403–409. https://doi.org/10.1006/anbo.1996.0361

Mahandran, V., Hakkim, H., Sinha, V., & Jain, M. (2023). Fruit scent as an indicator of ripeness status in 'bat fruits' to attract 'fruit bats': Chemical basis of chiropterochory. *Acta Ethologica*, *26*, 1–11. https://doi.org/10.1007/s10211-022-00405-1

Marwick, B., & Krishnamoorthy, K. (2019). Cvequality: Tests for the equality of coefficients of variation from multiple groups. https://github.com/benmarwick/cvequality

McFarlane, H. E., Döring, A., & Persson, S. (2014). The cell biology of cellulose synthesis. *Annual Review of Plant Biology*, *65*, 69–94. https://doi.org/10.1146/annurev-arplant-050213-040240

McMann, N., Peichel, A., & Savage, J. A. (2022). Early spring flowers rely on xylem hydration but are not limited by stem xylem conductivity. *New Phytologist*, *233*, 838–850. https://doi.org/10.1111/nph.17782

Metcalfe, H., Milne, A. E., Deledalle, F., & Storkey, J. (2020). Using functional traits to model annual plant community dynamics. *Ecology*, *101*, e03167. https://doi.org/10.1002/ecy.3167

Milla, R., & Reich, P. B. (2007). The scaling of leaf area and mass: The cost of light interception increases with leaf size. *Proceedings of the Royal Society B: Biological Sciences*, *274*, 2109–2115. https://doi.org/10.1098/rspb.2007.0417

Mu, X., & Chen, Y. (2021). The physiological response of photosynthesis to nitrogen deficiency. *Plant Physiology and Biochemistry*, *158*, 76–82. https://doi.org/10.1016/j.plaphy.2020.11.019

Neutelings, G. (2011). Lignin variability in plant cell walls: Contribution of new models. *Plant Science*, *181*, 379–386. https://doi.org/10.1016/j.plantsci.2011.06.012

Nilsson, T., & Gustavsson, K.-E. (2007). Postharvest physiology of 'aroma' apples in relation to position on the tree. *Postharvest Biology and Technology*, *43*, 36–46. https://doi.org/10.1016/j.postharvbio.2006.07.011

Oksanen, J., Simpson, G. L., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., O'Hara, R. B., Solymos, P., Stevens, M. H. H., Szoecs, E., Wagner, H., Barbour, M., Bedward, M., Bolker, B., Borcard, D., Carvalho, G., Chirico, M., Caceres, M. D., Durand, S., … Weedon, J. (2022). vegan: Community Ecology Package. https://github.com/vegandevs/vegan

Ostertag, R., Warman, L., Cordell, S., & Vitousek, P. M. (2015). Using plant functional traits to restore Hawaiian rainforest. *Journal of Applied Ecology*, *52*, 805–809. https://doi.org/10.1111/1365-2664.12413

Paquette, A., Fontaine, B., Berninger, F., Dubois, K., Lechowicz, M. J., Messier, C., Posada, J. M., Valladares, F., & Brisson, J. (2012). Norway maple displays greater seasonal growth and phenotypic plasticity to light than native sugar maple. *Tree Physiology*, *32*, 1339–1347. https://doi.org/10.1093/treephys/tps092

Paradis, E., & Schliep, K. (2019). Ape 5.0: An environment for modern phylogenetics and evolutionary analyses in R. *Bioinformatics*, *35*, 526–528. https://doi.org/10.1093/bioinformatics/bty633

Paź-Dyderska, S., Dyderski, M. K., Nowak, K., & Jagodziński, A. M. (2020). On the sunny side of the crown – Quantification of intra-canopy SLA variation among 179 taxa. *Forest Ecology and Management*, *472*, 118254. https://doi.org/10.1016/j.foreco.2020.118254

Paź-Dyderska, S., & Jagodziński, A. M. (2023). In search of a perfect trait set: A workflow presentation based on the conservation status assessment of Poland's dendroflora. *Ecology and Evolution*, *13*, e9979. https://doi.org/10.1002/ece3.9979

Paź-Dyderska, S., & Jagodziński, A. M. (2024). Low intra-canopy variability of floral traits in temperate woody plants. *Global Ecology and Conservation*, *54*, e03054. https://doi.org/10.1016/j.gecco.2024.e03054

Paź-Dyderska, S., Żytkowiak, R., & Jagodziński, A. M. (2022). Intra- and interspecific variability of non-structural carbohydrates and phenolic compounds in flowers of 70 temperate trees and shrubs. *Forests*, *13*, 1256. https://doi.org/10.3390/f13081256

Penone, C., Davidson, A. D., Shoemaker, K. T., Marco, M. D., Rondinini, C., Brooks, T. M., Young, B. E., Graham, C. H., & Costa, G. C. (2014). Imputation of missing data in life-history trait datasets: Which approach performs the best? *Methods in Ecology and Evolution*, *5*, 961–970. https://doi.org/10.1111/2041-210X.12232

Perez, T. M., Valverde-Barrantes, O., Bravo, C., Taylor, T. C., Fadrique, B., Hogan, J. A., Pardo, C. J., Stroud, J. T., Baraloto, C., & Feeley, K. J. (2019). Botanic gardens are an untapped resource for studying the functional ecology of tropical plants. *Philosophical Transactions of the Royal Society, B: Biological Sciences*, *374*, 20170390. https://doi.org/10.1098/rstb.2017.0390

Pérez-Harguindeguy, N., Díaz, S., Garnier, E., Lavorel, S., Poorter, H., Jaureguiberry, P., Bret-Harte, M. S., Cornwell, W. K., Craine, J. M., Gurvich, D. E., Urcelay, C., Veneklaas, E. J., Reich, P. B., Poorter, L., Wright, I. J., Ray, P., Enrico, L., Pausas, J. G., de Vos, A. C., … Cornelissen, J. H. C. (2013). New handbook for standardised measurement of plant functional traits worldwide. *Australian Journal of Botany*, *61*, 167. https://doi.org/10.1071/BT12225

Pers-Kamczyc, E., Tyrała-Wierucka, Ż., Rabska, M., Wrońska-Pilarek, D., & Kamczyc, J. (2020). The higher availability of nutrients increases the production but decreases the quality of pollen grains in *Juniperus communis* L. *Journal of Plant Physiology*, *248*, 153156. https://doi.org/10.1016/j.jplph.2020.153156

Petchey, O. L., & Gaston, K. J. (2006). Functional diversity: Back to basics and looking forward. *Ecology Letters*, *9*, 741–758. https://doi.org/10.1111/j.1461-0248.2006.00924.x

Petruzzellis, F., Palandrani, C., Savi, T., Alberti, R., Nardini, A., & Bacaro, G. (2017). Sampling intraspecific variability in leaf functional traits: Practical suggestions to maximize collected information. *Ecology and Evolution*, *7*, 11236–11245. https://doi.org/10.1002/ece3.3617

Poorter, H., Niinemets, Ü., Poorter, L., Wright, I. J., & Villar, R. (2009). Causes and consequences of variation in leaf mass per area (LMA): A meta-analysis. *New Phytologist*, *182*, 565–588. https://doi.org/10.1111/j.1469-8137.2009.02830.x

Poorter, H., Pepin, S., Rijkers, T., de Jong, Y., Evans, J. R., & Körner, C. (2006). Construction costs, chemical composition and payback time of high- and low-irradiance leaves. *Journal of Experimental Botany*, *57*, 355–371. https://doi.org/10.1093/jxb/erj002

Pyšek, P., Manceur, A. M., Alba, C., McGregor, K. F., Pergl, J., Štajerová, K., Chytrý, M., Danihelka, J., Kartesz, J., Klimešová, J., Lučanová, M., Moravcová, L., Nishino, M., Sádlo, J., Suda, J., Tichý, L., & Kühn, I. (2015). Naturalization of central European plants in North America: Species traits, habitats, propagule pressure, residence time. *Ecology*, *96*, 762–774. https://doi.org/10.1890/14-1005.1

Qin, X., Liang, W., Liu, Z., Liu, M., Baskin, C. C., Baskin, J. M., Xin, Z., Wang, Z., & Zhou, Q. (2022). Plant canopy may promote seed dispersal by wind. *Scientific Reports*, *12*, 63. https://doi.org/10.1038/s41598-021-03402-9

R Core Team. (2023). R: A language and environment for statistical computing.

Reich, P. B. (2014). The world-wide 'fast–slow' plant economics spectrum: A traits manifesto. *Journal of Ecology*, *102*, 275–301. https://doi.org/10.1111/1365-2745.12211

Reich, P. B., Ellsworth, D. S., & Walters, M. B. (1998). Leaf structure (specific leaf area) modulates photosynthesis-nitrogen relations: Evidence from within and across species and functional groups. *Functional Ecology*, *12*, 948–958. https://doi.org/10.1046/j.1365-2435.1998.00274.x

Revell, L. J. (2020). Phytools: Phylogenetic tools for comparative biology (and other things). https://github.com/liamrevell/phytools

Roddy, A. B. (2019). Energy balance implications of floral traits involved in pollinator attraction and water balance. *International Journal of Plant Sciences*, *180*, 944–953. https://doi.org/10.1086/705586

Roddy, A. B., Brodersen, C. R., & Dawson, T. E. (2016). Hydraulic conductance and the maintenance of water balance in flowers. *Plant, Cell & Environment*, *39*, 2123–2132. https://doi.org/10.1111/pce.12761

Roddy, A. B., Martínez-Perez, C., Teixido, A. L., Cornelissen, T. G., Olson, M. E., Oliveira, R. S., & Silveira, F. A. O. (2021). Towards the flower economics spectrum. *New Phytologist*, *229*, 665–672. https://doi.org/10.1111/nph.16823

Rodríguez, A., Alquézar, B., & Peña, L. (2013). Fruit aromas in mature fleshy fruits as signals of readiness for predation and seed dispersal. *New Phytologist*, *197*, 36–48. https://doi.org/10.1111/j.1469-8137.2012.04382.x

Santiago, J. P., & Sharkey, T. D. (2019). Pollen development at high temperature and role of carbon and nitrogen metabolites. *Plant, Cell & Environment*, *42*, 2759–2775. https://doi.org/10.1111/pce.13576

Santos, T. (2018). PVR: Phylogenetic eigenvectors regression and Phylogentic Signal-Representation Curve. https://CRAN.R-project.org/package=PVR

Sapir, Y., Brunet, J., Byers, D. L., Imbert, E., Schönenberger, J., & Staedler, Y. (2019). Floral evolution: Breeding systems, pollinators, and beyond. *International Journal of Plant Sciences*, *180*, 929–933. https://doi.org/10.1086/706240

Siefert, A., Violle, C., Chalmandrier, L., Albert, C. H., Taudiere, A., Fajardo, A., Aarssen, L. W., Baraloto, C., Carlucci, M. B., Cianciaruso, M. V., de L Dantas, V., de Bello, F., Duarte, L. D., Fonseca, C. R., Freschet, G. T., Gaucherand, S., Gross, N., Hikosaka, K., Jackson, B., … Wardle, D. A. (2015). A global meta-analysis of the relative extent of intraspecific trait variation in plant communities. *Ecology Letters*, *18*, 1406–1419. https://doi.org/10.1111/ele.12508

Snell, R. S., Beckman, N. G., Fricke, E., Loiselle, B. A., Carvalho, C. S., Jones, L. R., Lichti, N. I., Lustenhouwer, N., Schreiber, S. J., Strickland, C., Sullivan, L. L., Cavazos, B. R., Giladi, I., Hastings, A., Holbrook, K. M., Jongejans, E., Kogan, O., Montaño-Centellas, F., Rudolph, J., … Schupp, E. W. (2019). Consequences of intraspecific variation in seed dispersal for plant demography, communities, evolution and global change. *AoB Plants*, *11*, plz016. https://doi.org/10.1093/aobpla/plz016

Stekhoven, D. J., & Bühlmann, P. (2012). MissForest - nonparametric missing value imputation for mixed-type data. *Bioinformatics*, *28*, 112–118. https://doi.org/10.1093/bioinformatics/btr597

Stewart, K., Carmona, C. P., Clements, C., Venditti, C., Tobias, J. A., & González-Suárez, M. (2023). Functional diversity metrics can perform well with highly incomplete data sets. *Methods in Ecology and Evolution*, *14*, 2856–2872. https://doi.org/10.1111/2041-210X.14202

Stournaras, K. E., & Schaefer, H. M. (2017). Does flower and fruit conspicuousness affect plant fitness? Contrast, color coupling and the interplay of pollination and seed dispersal in two *Vaccinium* species. *Evolutionary Ecology*, *31*, 229–247. https://doi.org/10.1007/s10682-016-9864-1

Svensson, L. (1992). Estimates of hierarchical variation in flower morphology in natural populations of *Scleranthus annuus* (Caryophyllaceae), an inbreeding annual. *Plant Systematics and Evolution*, *180*, 157–180. https://doi.org/10.1007/BF00941149

Tal, O. (2011). Flowering phenological pattern in crowns of four temperate deciduous tree species and its reproductive implications. *Plant Biology*, *13*, 62–70. https://doi.org/10.1111/j.1438-8677.2010.00386.x

te Beest, M., Esler, K. J., & Richardson, D. M. (2015). Linking functional traits to impacts of invasive plant species: A case study. *Plant Ecology*, *216*, 293–305. https://doi.org/10.1007/s11258-014-0437-5

Teixido, A. L., Barrio, M., & Valladares, F. (2016). Size matters: Understanding the conflict faced by large flowers in Mediterranean environments. *The Botanical Review*, *82*, 204–228. https://doi.org/10.1007/s12229-016-9168-8

Trugman, A. T., Anderegg, L. D. L., Wolfe, B. T., Birami, B., Ruehr, N. K., Detto, M., Bartlett, M. K., & Anderegg, W. R. L. (2019). Climate and plant trait strategies determine tree carbon allocation to leaves and mediate future forest productivity. *Global Change Biology*, *25*, 3395–3405. https://doi.org/10.1111/gcb.14680

Tustin, D. S., Hirst, P. M., & Warrington, I. J. (1988). Influence of orientation and position of fruiting laterals on canopy light penetration, yield, and fruit quality of 'Granny Smith' apple. *Journal of the American Society for Horticultural Science*, *113*, 693–699. https://doi.org/10.21273/JASHS.113.5.693

Ueda, M. U., Mizumachi, E., & Tokuchi, N. (2011). Foliage nitrogen turnover: Differences among nitrogen absorbed at different times by *Quercus serrata* saplings. *Annals of Botany*, *108*, 169–175. https://doi.org/10.1093/aob/mcr092

Valladares, F., Wright, S. J., Lasso, E., Kitajima, K., & Pearcy, R. W. (2000). Plastic phenotypic response to light of 16 congeneric shrubs from a Panamanian rainforest. *Ecology*, *81*, 1925–1936. https://doi.org/10.1890/0012-9658(2000)081[1925:PPRTLO]2.0.CO;2

van Bodegom, P. M., Douma, J. C., & Verheijen, L. M. (2014). A fully traits-based approach to modeling global vegetation distribution. *Proceedings of the National Academy of Sciences of the United States of America*, *111*, 13733–13738. https://doi.org/10.1073/pnas.1304551110

Van der Niet, T., Peakall, R., & Johnson, S. D. (2014). Pollinator-driven ecological speciation in plants: New evidence and future perspectives. *Annals of Botany*, *113*, 199–212. https://doi.org/10.1093/aob/mct290

van Kleunen, M., Meier, A., Saxenhofer, M., & Fischer, M. (2008). Support for the predictions of the pollinator-mediated stabilizing selection hypothesis. *Journal of Plant Ecology*, *1*, 173–178. https://doi.org/10.1093/jpe/rtn017

Violle, C., Navas, M.-L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., & Garnier, E. (2007). Let the concept of trait be functional! *Oikos*, *116*, 882–892. https://doi.org/10.1111/j.0030-1299.2007.15559.x

Westerband, A. C., Funk, J. L., & Barton, K. E. (2021). Intraspecific trait variation in plants: A renewed focus on its role in ecological processes. *Annals of Botany*, *127*, 397–410. https://doi.org/10.1093/aob/mcab011

Westoby, M. (1998). A leaf-height-seed (LHS) plant ecology strategy scheme. *Plant and Soil*, *199*, 213–227. https://doi.org/10.1023/A:1004327224729

Wickham, H., Chang, W., Henry, L., Pedersen, T. L., Takahashi, K., Wilke, C., Woo, K., & Yutani, H. (2020). ggplot2: Create Elegant Data Visualisations Using the Grammar of Graphics. https://ggplot2.tidyverse.org

Wickham, H., Francois, R., Henry, L., & Müller, K. (2020). dplyr: A Grammar of Data Manipulation. https://dplyr.tidyverse.org

Wright, I. J., Reich, P. B., Westoby, M., Ackerly, D. D., Baruch, Z., Bongers, F., Cavender-Bares, J., Chapin, T., Cornelissen, J. H. C., Diemer, M., Flexas, J., Garnier, E., Groom, P. K., Gulias, J., Hikosaka, K., Lamont, B. B., Lee, T., Lee, W., Lusk, C., … Villar, R. (2004). The worldwide leaf economics spectrum. *Nature*, *428*, 821–827. https://doi.org/10.1038/nature02403

Wyka, T. P., Oleksyn, J., Żytkowiak, R., Karolewski, P., Jagodziński, A. M., & Reich, P. B. (2012). Responses of leaf structure and photosynthetic properties to intra-canopy light gradients: A common garden test with four broadleaf deciduous angiosperm and seven evergreen conifer tree species. *Oecologia*, *170*, 11–24. https://doi.org/10.1007/s00442-012-2279-y

Ye, J. Y., Tian, W. H., & Jin, C. W. (2022). Nitrogen in plants: From nutrition to the modulation of abiotic stress adaptation. *Stress Biology*, *2*, 4. https://doi.org/10.1007/s44154-021-00030-1

Zhang, F.-P., & Brodribb, T. J. (2017). Are flowers vulnerable to xylem cavitation during drought? *Proceedings of the Royal Society B: Biological Sciences*, *284*, 20162642. https://doi.org/10.1098/rspb.2016.2642

Zhang, F.-P., Yang, Y.-J., Yang, Q.-Y., Zhang, W., Brodribb, T. J., Hao, G.-Y., Hu, H., & Zhang, S.-B. (2017). Floral mass per area and water maintenance traits are correlated with floral longevity in *Paphiopedilum* (Orchidaceae). *Frontiers in Plant Science*, *8*, 501.

Zhao, D., Reddy, K. R., Kakani, V. G., & Reddy, V. R. (2005). Nitrogen deficiency effects on plant growth, leaf photosynthesis, and hyperspectral reflectance properties of sorghum. *European Journal of Agronomy*, *22*, 391–403. https://doi.org/10.1016/j.eja.2004.06.005

Zheng, L., Ives, A. R., Garland, T., Larget, B. R., Yu, Y., & Cao, K. (2009). New multivariate tests for phylogenetic signal and trait correlations applied to ecophysiological phenotypes of nine *Manglietia* species. *Functional Ecology*, *23*, 1059–1069. https://doi.org/10.1111/j.1365-2435.2009.01596.x

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Paź-Dyderska, S., & Jagodziński, A. M. (2024). Potential of reproductive traits in functional ecology: A quantitative comparison of variability in floral, fruit, and leaf traits. *Ecology and Evolution*, *14*, e11690. https://doi.org/10.1002/ece3.11690

Table S1. Results of trait-wise Krishnamoorthy and Lee's (2014) modified signed-likelihood ratio tests. Upper part – test statistics, lower part – p-values.

	SLA	Leaf C	Leaf N	Leaf C:N	Flower C	Flower N	Flower C:N	Flower length	Flower width	Flower dry mass	Fruit length	Fruit diameter	Fruit dry mass	Fruit C	Fruit N	Fruit C:N
SLA	-	260.114	8.113	8.323	289.565	1.695	0.932	47.300	38.414	96.755	19.636	16.455	59.589	0.009	58.869	11.675
Leaf C	<0.001	-	187.414	186.341	2.151	232.275	225.953	392.314	356.026	399.808	297.513	312.805	412.056	218.084	395.157	282.589
Leaf N	0.278	<0.001	-	0.084	210.497	2.946	3.819	87.185	77.979	147.600	45.344	40.316	88.414	6.156	98.742	32.802
Leaf C:N	0.197	<0.001	1.000	-	201.835	2.223	3.064	80.030	71.894	165.882	50.333	43.256	101.514	5.501	94.632	29.184
Flower C	<0.001	1.000	<0.001	<0.001	-	201.766	222.964	371.993	344.968	391.629	272.082	291.973	359.149	205.748	365.052	295.005
Flower N	1.000	<0.001	1.000	1.000	<0.001	-	0.060	59.089	48.346	107.254	27.501	24.128	78.382	0.984	86.744	18.762
Flower C:N	1.000	<0.001	1.000	1.000	<0.001	1.000	-	55.787	50.686	101.036	26.812	23.748	75.836	0.640	78.306	14.346
Flower length	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	-	0.804	13.381	1.598	2.804	3.642	26.065	3.666	6.355
Flower width	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	1.000	-	21.394	0.422	1.130	7.334	17.215	6.323	3.125
Flower dry mass	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	0.034	0.003	-	9.735	12.544	0.496	46.881	0.582	15.545
Fruit length	0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	1.000	1.000	0.177	-	0.137	6.393	11.048	6.968	0.981
Fruit diameter	0.005	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	1.000	1.000	0.016	1.000	-	9.296	9.276	8.696	0.437
Fruit dry mass	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	1.000	0.500	1.000	0.327	0.197	-	35.227	0.081	12.623
Fruit C	1.000	<0.001	0.897	1.000	<0.001	1.000	1.000	<0.001	0.002	<0.001	0.027	0.125	<0.001	-	33.070	6.838
Fruit N	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	1.000	0.624	1.000	0.654	0.189	1.000	<0.001	-	13.231
Fruit C:N	0.122	<0.001	<0.001	<0.001	<0.001	0.002	0.003	0.981	1.000	0.004	1.000	1.000	0.038	0.752	0.036	-

Table S2. Results of phylogenetic paired t-tests for traits PI, applied for each pair of traits. Upper part – test statistics, lower part – p-values.

	SLA	Leaf C	Leaf N	Leaf C:N	Flower C	Flower N	Flower C:N	Flower length	Flower width	Flower dry mass	Fruit length	Fruit diameter	Fruit dry mass	Fruit C	Fruit N	Fruit C:N
SLA	-	13.680	9.072	8.360	10.081	9.430	9.404	9.014	6.175	4.236	7.294	7.036	4.551	7.658	3.864	3.854
Leaf C	<0.001	-	-8.897	-8.625	5.491	-6.874	-6.956	-5.049	-3.247	-7.469	-3.622	-1.815	-7.380	-0.389	-3.810	-3.902
Leaf N	<0.001	<0.001	-	0.320	9.904	0.019	0.038	1.126	-0.519	-2.712	3.278	3.723	-1.383	4.554	-0.191	-0.259
Leaf C:N	<0.001	<0.001	1.000	-	9.500	-0.034	-0.016	1.054	-0.557	-2.735	3.202	3.749	-1.320	4.473	-0.161	-0.237
Flower C	<0.001	<0.001	<0.001	<0.001	-	-7.869	-7.970	-5.442	-3.111	-8.497	-6.188	-4.636	-8.645	-2.356	-4.320	-4.405
Flower N	<0.001	<0.001	1.000	1.000	<0.001	-	0.199	1.689	-0.337	-2.970	1.989	2.518	-2.296	3.505	-0.309	-0.407
Flower C:N	<0.001	<0.001	1.000	1.000	<0.001	1.000	-	1.688	-0.382	-3.004	2.033	2.546	-2.262	3.536	-0.288	-0.386
Flower length	<0.001	0.001	1.000	1.000	<0.001	1.000	1.000	-	-1.663	-4.041	0.884	1.243	-3.366	2.466	-1.437	-1.519
Flower width	<0.001	0.243	1.000	1.000	0.363	1.000	1.000	1.000	-	-3.302	0.952	1.303	-3.612	2.617	-1.740	-1.821
Flower dry mass	0.011	<0.001	0.958	0.915	<0.001	0.500	0.475	0.021	0.211	-	2.963	3.118	0.081	4.029	0.653	0.619
Fruit length	<0.001	0.160	0.360	0.419	<0.001	1.000	1.000	1.000	1.000	0.709	-	0.494	-6.822	2.405	-2.509	-2.610
Fruit diameter	<0.001	1.000	0.123	0.117	0.012	1.000	1.000	1.000	1.000	0.496	1.000	-	-7.802	2.080	-2.612	-2.740
Fruit dry mass	0.014	<0.001	1.000	1.000	<0.001	1.000	1.000	0.291	0.162	1.000	<0.001	<0.001	-	6.562	0.852	0.771
Fruit C	<0.001	1.000	0.014	0.018	1.000	0.214	0.203	1.000	1.000	0.058	1.000	1.000	<0.001	-	-3.130	-3.229
Fruit N	0.089	0.100	1.000	1.000	0.028	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.489	-	-0.587
Fruit C:N	0.090	0.081	1.000	1.000	0.022	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.397	1.000	-

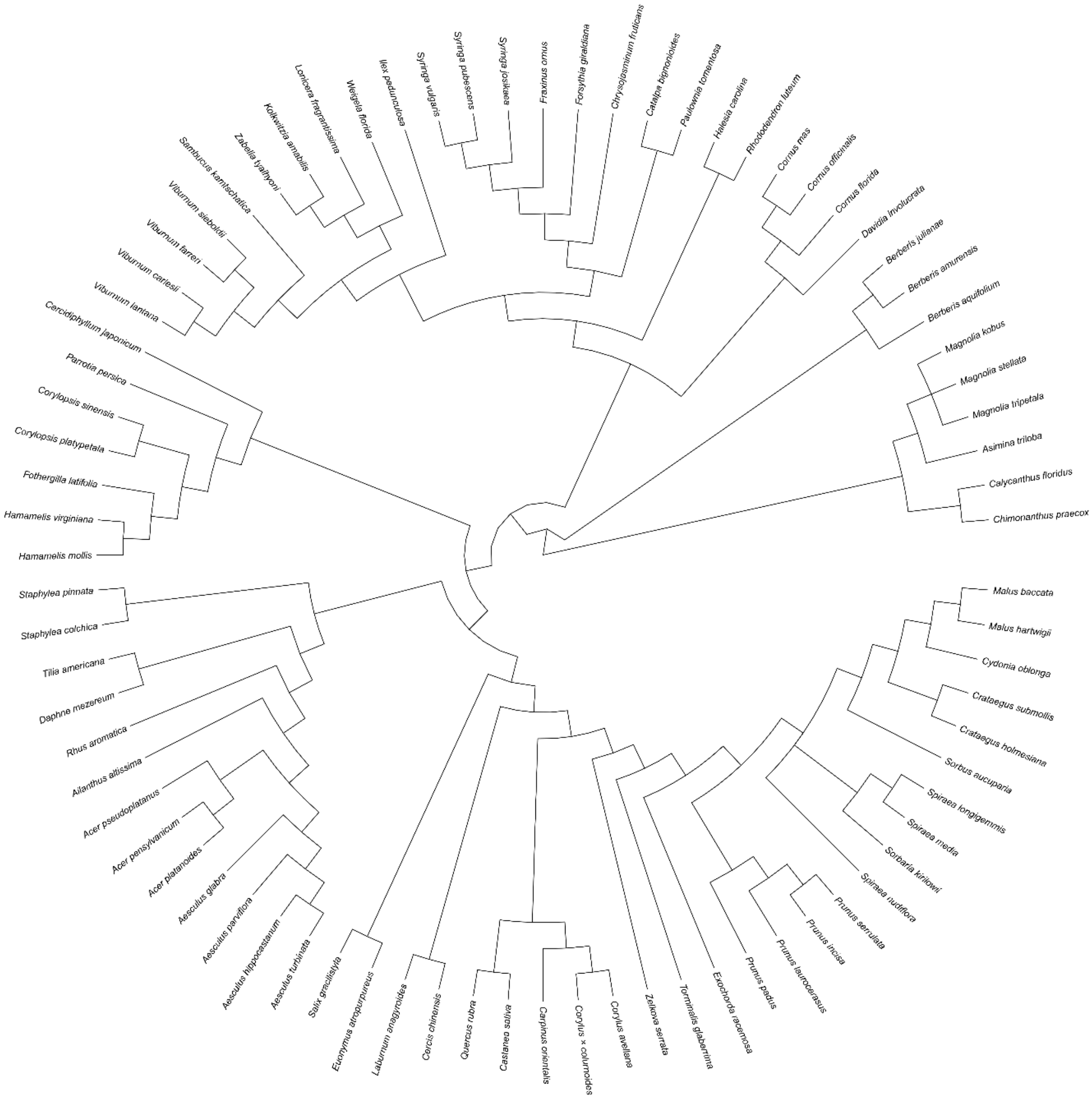


Fig. S1. Phylogenetic tree visualizing the evolutionary history of analyzed species.